ABOVEGROUND PRIMARY PRODUCTIVITY IN FOREST ECOSYSTEMS AS A FUNCTION OF SPECIES RICHNESS AND COMPOSITION

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CONTENTS

SUMMARY

We are living through one of the largest species extinction events in world history. The relevance of diversity for world ecosystems and their functioning is therefore one of the major topics in current ecological research. Evidence in grassland experiments demonstrates a positive diversity−productivity relationship. Due to logistic difficulties, forest ecosystems have been much less studied, even though their global relevance in terms of diversity and carbon assimilation is particularly high. In this project we investigate the aboveground diversity−aboveground productivity relationship of tree species communities in subtropical forests.

In **chapter 1** I report results from a comparative study, in which we assessed standing biomass and growth as a function of species richness, functional and phylogenetic diversity and evenness in natural subtropical forests of different successional stages over two growing seasons (2008–2010). I measured two cohorts of individuals: all individuals ≥ 10 cm DBH (diameter at breast height) and all individuals 3 cm ≤ DBH < 10 cm. Tree basal area and tree basal area increment at plot level were positively related with species richness and functional and phylogenetic diversity, whereas growth was negatively related to successional stage. Species richness and evenness showed a negative correlation, thus basal area and basal area increment were negatively correlated with evenness. The diversity effect was determined by larger mean individual sizes and higher densities in more diverse plots.

In **Chapter 2** I investigated the effect of species richness and density on sapling biomass allocation, crown architecture and branch demography. I planted an experiment with a pool of four tree species. The four species were planted in monoculture, in all six 2-species mixtures and in 4-species mixture. I had in addition a low-, an intermediate- and a high-density level of individuals per plot. Species richness enhanced pruning and branch turnover, but growth was mainly determined by individual species identity. I conclude that crown architecture and branch

demography were mainly controlled by light competition. I found intraspecific competition to be stronger than interspecific competition in two species.

In **Chapter 3** I used an experimental approach to assess biomass of sapling communities as a function of species richness in two light conditions. I planted an experiment with three species pools, each of four species. Within each species pool I planted four monocultures, six 2-species mixtures and the 4-species mixture in direct sunlight and in a shade cage. Plots were planted in a four-by-four array of sixteen individuals per square meter. Eighteen months after planting the aboveground section of the four central individuals was harvested, dried and weighed. I found a positive effect of species richness on mixture biomass in the two light treatments. The species diversity effect was caused by an increased likelihood of finding individuals of the dominant species of each species pool in the more diverse mixtures (so-called sampling effect of biodiversity). Biomass in the shaded mixtures was lower than in direct sunlight, due to lowered individual growth and increased mortality.

In **Chapter 4**, I analyzed in depth the 2-species mixtures presented in Chapter 3 by exploring the effect of species identity, species composition and functional distance between species on aboveground biomass and on biodiversity effects, in particular selection and complementarity effects. I found a strong effect of species identity and of functional distance between the species on the aboveground biomass of the mixtures, net biodiversity and selection effects. I used a mechanistic diallel analysis to assess the effect of general and specific combining ability of species on mixture performance and found a positive correlation between functional distance and specific combining ability.

Overall, my work shows that a positive diversity−productivity relationship also occurs in communities of tree species, both in mature natural stands and in experimental communities of samplings. The results from the sapling experiment furthermore demonstrate the relevance of

species identity and species differences for mixture performance. The diversity−productivity relationship was consistent under different light conditions, demonstrating its generality.

ZUSAMMENFASSUNG

Aktuell erleben wir eines der grössten Artensterben der Weltgeschichte. Die Bedeutung der Biodiversität für die Ökosysteme der Erde und für deren Funktionen ist daher eines der wichtigsten Themen in der ökologischen Forschung. Biodiversitätsexperimente mit Wiesenpflanzen zeigen einen positiven Zusammenhang zwischen Artenvielfalt und mehreren Ökosystemfunktionen, wie zum Beispiel der Produktivität. Waldökosysteme, hingegen, wurden aufgrund logistischer Schwierigkeiten viel weniger untersucht, trotz ihrer globalen Relevanz in Bezug auf Biodiversität und Kohlenstoffassimilation. In diesem Projekt untersuchten wir den Zusammenhang zwischen der oberirdischen Produktivität und der Biodiversität von Baumarten in südtropischen Wäldern.

In **Kapitel 1** berichte ich über die Ergebnisse einer vergleichenden Studie in der wir erstens die Biomasse und das Baumwachstum als Funktion der Artenzahl, zweitens die funktionelle und phylogenetische Vielfalt und drittens die Gleichmässigkeit der Artenverteilung („Evenness“) in natürlichen südtropischen Wäldern mit verschiedenen Sukzessionstadien über eine Wachstumsperiode von 2008-2010 untersuchten. Ich mass zwei Kohorten von Bäumen: alle Bäume mit einem Brusthöhendurchmesser (BHD) von $\geq$ 10 cm und alle Bäume mit einem BHD von 3 cm $\leq$ BHD < 10 cm. Die Basalfläche und das Wachstum steigen mit grösserer Artenzahl, sowie mit der funktionellen und phylogenetischen Diversität, während das Wachstum mit zunehmendem Sukzessionsstadium abnimmt. Die Artenzahl und die Gelichmässigkeit der Artenverteilung korrelieren negativ. Der Biodiversitätseffekt wurde von grösseren Stammdurchmessern und höheren Baumdichten in artenreicheren Versuchsflächen bestimmt.

In **Kapitel 2** untersuchte ich den Effekt von Artenzahl und Baumdichte auf die Biomasseallokation, die Baumkronenarchitektur und die Zweigdemographie von Schösslingen. Ich pflanzte einen Versuch mit vier Baumarten in vier Monokulturen, sechs 2-Arten-Mischungen und einer 4-Arten-Mischung. Zusätzlich pflanzte ich eine niedrige, eine intermediäre und eine

hohe Pflanzendichte pro Plot. Die Artenzahl erhöhte den Astumsatz, aber das Wachstum wurde vor allem von der Identität einzelner Arten bestimmt. Anscheinend wird die Baumkronenarchitektur und die Zweigdemographie vom Wettbewerb um Licht bestimmt. Weiter fand ich eine stärkere intraspezifische als interspezifische Konkurrenz bei zwei von vier Arten.

In **Kapitel 3** wendete ich einen experimentellen Ansatz an, um die Biomasse von Jungbeständen als Funktion der Baumartenzahl unter zwei Lichtbedingungen zu messen. Ich pflanzte einen Versuch mit drei Artenpools, jeder bestehend aus vier Baumarten. Innerhalb jedes Artenpools pflanzte ich vier Monokulturen, sechs 2-Arten-Mischkulturen und eine 4-Arten-Mischkultur, sowohl in direktem Sonnenlicht wie auch unter Beschattung. Die Versuchsflächen wurden in vier Reihen à vier Pflanzen gepflanzt, das heisst 16 Individuen pro Quadratmeter (1 m^2). Achtzehn Monate später erntete ich die oberirdischen Pflanzenteile der vier im Zentrum positionierten Pflanzen und ermittelte deren Trockengewicht. Auch hier fand ich einen positiven Effekt der Artenzahl auf die Biomasse unter beiden Lichtbedingungen. Der Biodiversitätseffekt war dabei die Folge der Wahrscheinlichkeit, dass Pflanzen von dominanten Arten jedes Artenpools öfters in den artenreicheren Mischungen gefunden werden (Selektionseffekt). Die Biomasse in den schattigen Mischungen war niedriger als die Biomasse bei direkter Sonneneinstrahlung, dies aufgrund artspezifischer Unterschiede im Überleben und individuellen Wachstum.

In **Kapitel 4** analysierte ich die 2-Arten-Mischkulturen aus Kapitel 3 noch genauer, um den Effekt der Artenidentität, der Artenkombination und der funktionellen Distanz zwischen den Arten auf die oberirdische Biomasse, sowie deren Beziehung zu Selektions- und Komplementaritätseffekten zu bestimmen. Ich untersuchte die achtzehn 2-Arten-Mischungen unter beiden Lichtbedingungen. Dabei fand ich einen starken Einfluss der Artenidentität, und

insbesondere der funktionellen Distanz zwischen den Arten innerhalb der Mischungen auf die gemessenen Biodiversitätseffekte. Ich verwendete eine mechanistische Diallel-Analyse, um die Auswirkung der spezifischen Arten in Mischkulturen zu bewerten und, um die Korrelation der funktionellen Distanz mit der spezifischen Kombinationsfähigkeit der Arten zu analysieren.

Ich fand einen positiven Zusammenhang von Diversität und Produktivität in Gemeinschaften von Baumarten, unter natürlichen und experimentellen Bedingungen. Meine Ergebnisse unter experimentellen Bedingungen zeigen die Relevanz der Artzusammensetzung: Dominante Arten und die funktionelle Distanz zwischen Arten in der Gemeinschaft erklären die Unterschiede in der Gesamtbiomasse und den Biodiversitätseffekten zwischen verschiedenen Baumgemeinschaften. Der Zusammenhang zwischen Diversität und Produktivität war gleichbleibend unter verschiedenen Lichtbedingungen. Zusammenfassend unterstreichen diese Resultate die grosse Bedeutung der Erhaltung artenreicher Wälder für die Biomasseproduktion und damit die Kohlenstoffspeicherung.

GENERAL INTRODUCTION

Biodiversity loss and its implication for ecosystems

We are living under the threat of one of the worst extinction events in world's history (Chapin *et al*. 2000, McCann 2000, Barnosky *et al*. 2011). Biodiversity loss implies changes in ecosystem structures, which affect their main processes (Chapin *et al*. 2000), namely biogeochemical activities, which determine any part of nutrient cycling (Naeem & Wright 2003). The concern regarding biodiversity effects on ecosystem functions and how these changes may affect ecosystem services shaped one of the most important ecological questions of the last decades: what are the effects of biodiversity loss on vital ecosystem functions (Loreau *et al*. 2001, Naeem 2002, Balvanera *et al*. 2006, Cardinale *et al*. 2012)?

Biodiversity ecosytem functioning (BEF), has developed as a research field in response to this question, including several approaches, measures of diversity, ecosystem types, and ecosystem functions. After roughly 20 years of research, several ecosystem processes have been evaluated and a list of conclusions has been established (Balvanera *et al*. 2006, Cardinale *et al*. 2006, Cardinale *et al*. 2012).

Biodiversity is defined by the convention on biological diversity as the "variability among living organisms from all sources including terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, among species, and of ecosystems (FAO 2010). As measurement of diversity BEF research has included different kind of measurements, from simple and easy to measure, such as species richness, to more comprehensive and informative such as Shannon index and evenness, which besides species number considers relative abundance. Other spread diversity measurements are the phylogenetic diversity and the functional diversity (Balvanera *et al*. 2006). Phylogenetic diversity refers to the evolutionary distance between the species, measured as the total distance of the phylogenetic dendrogram (May 1990), and the functional diversity refers to the

multi-dimensional trait heterogeneity encompassed within the species which compose the ecosystem. Functional diversity has been measured through several indexes (Mouchet *et al.* 2010); from simple calculations based on the grouping of relevant functional traits (Roscher *et al*. 2004), to the calculations of the distances from functional dendrograms (Petchey & Gaston 2002), as in the case of the phylogenetic diversity.

A positive diversity−productivity relationship, one of the most common ecosystem functions assesed has been experimentally demonstrated. Other ecosystems functions, such as stability at the community level, nutrient cycling and regulation of biological diversity, are positively affected by diversity also (Hooper *et al*. 2005, Balvanera *et al*. 2006, Cardinale *et al*. 2006). Diversity effects varied according to study-type. For instance, analysis of better controlled settings, show stronger results; analysis at population level fluctuated more with increasing diversity; analysis show stronger effects at community level, than at ecosystem level, and show negative effects at population level; and, in studies considering several trophic levels, the effect declines between the manipulated and the measured level, if biodiversity effects are productivity-related (Balvanera *et al*. 2006).

It has been discussed if diversity effects are not more than product of one or few species, or a particular composition which determines the best assemblage for a define function. However, besides the diversity effects on individual ecosystem processes, different ecosystem processes require different sets of species, at different times, in different places, and, under different environmental settings. This implies that extinction of any species would decrease ecosystem function in at least one functional context (Yachi & Loreau 1999, Isbell *et al*. 2011, Aerts & Honnay 2011).

Although the progresses on BEF determine the relevance of diversity for particular ecosystem function, there are several uncertainties and doubts, open to be solved. Most of the experiments

have been carried out in grasslands (Balvanera *et al*. 2006, Scherer-Lorenzen *et al*. 2007, Nadrowski *et al*. 2011) or microcosm experiments (Balvanera *et al.* 2006) and other ecosystem and community types are underrepresented within the results. In general, studies on ecosystems with short time spans and small sizes, are more common than studies on ecosystems with long time spans and relevant at larger areas, as it is relatively easier to set controls over them and to evaluate over relevant time spans.

On the other hand, some of these experiments, such as the ones with grasslands, in which entities present clonal growth, imply the challenge of defining individual entities. Individual densities and growth can thus be also a confounding factor, if the effective individual number varies over richness levels; substitutive designs are suggested to avoid this particular difficulty (Balvanera *et al.* 2006).

Diversity effect measurements and mechanisms

The mechanistic causes considered to promote diversity effects, are broadly divided between selection and complementarity effects. Selection effects are caused by particular species or set of species, with high performance that dominate (over-perform) the community. Complementarity effects consider niche complementarity (differentiation in the use of resources, i.e light availability and nutrient uptake) and positive interactions (Loreau & Hector 2001, Spehn *et al*. 2005). Complementarity and selection effects can occur, either independent one of the other, or simultaneously (Loreau & Hector 2001).

Analysis on biodiversity effects included, in addition to direct comparison of less diverse and more diverse communities, measurements to define effects on the particular species. This permits to determine the occurrence of overyielding and performance of particular species (these measurements are commonly used to express the values of biomass or yield of the community; however the calculations can be applied to other ecosystem processes). The relative yield total

(*RYT*) and the proportional deviation of the observed total yield from its expected value (D_T) are standardized measurements, used to compare monocultures against diverse mixtures. Likewise, the relative yield of the species (RY_i) and the proportional deviation of the target species yield from its expected value (D_i), allow comparing performance of particular species (Wardle *et al*. 1997, Hector 1998, Loreau 1998).

Nevertheless, these measurements fail to determine effectively by themselves, which mechanisms are responsible for the diversity effects. The development of the additive partition of biodiversity effects (Hector & Loreau 2001) allows differentiating the selection and the complementarity effects. This methodological approach measures the selection effect based on the Price's general theory of selection (Price 1995) by calculating covariance of the relative yields and the monoculture biomass of the species; the complementarity effect measures changes in the relative yield form the mixtures. In addition, a net effect (i.e. the effective diversity effect) is calculated as the sum of the selection and the complementarity effects; all three effects can be positive or negative. If the selection and the net effect have opposite sign, they can cancel each other.

BEF in forest ecosystems

BEF studies are biased towards grassland experiments and other small to medium scale ecosystems and most of the conclusions were determined out of these particular ecosystems. Forests on the other hand are underrepresented in BEF research (Balvanera *et al*. 2006, Nadrowski *et al.* 2011).

Forests are key worldwide ecosystems; they contain more than half of terrestrial plants and animals; cover roughly 31% of total land area, and are responsible for more than two thirds of the net primary productivity (FAO 2010). As a major world ecosystem, forests are important regulators of world and regional relevant ecosystem processes and provide multiple resources

(i.e. food, medicine, wood) to human populations (Aerts & Honnay 2011). Forests have been used and managed during most of human story; and, as societies develop they are managed and replaced for other land uses. As human population is growing rapidly, particularly in undeveloped regions, such as the tropics, forest area has decline stronger in these highly diverse and productive ecosystems (Vitousek *et al*. 1997, Wright & Muller-Landau 2006, Aerts & Honnay 2011). World forest cover reduced 8.3 and 5.2 million hectares on average per year during the 90's and first decade of the millennium, respectively (FAO 2010). Primary forests cover area estimates, decreased at a rate of 0.4% per year during the first decade of the millenium, mainly because it was reclassified as other forest types, due to the management practices, as for example selective logging and other human productive activities (FAO 2010).

Forests are heterogeneous; their structure depends of the geophysical position (Holdridge 1947), but also of their particular life-history. Forest ecosystem processes are affected by their internal structure, and variables such as diversity or successional stage are expected to influence these processes (Brown *et al*. 1991, Balvanera & Aguirre 2006). There is a great uncertainty about the effects and magnitudes to which the decline of forest area, quality and diversity (Barlow *et al*. 2007, FAO 2010) will be on basic ecological processes, at local, regional and global levels. It has been established that forest diversity can have effects on ecosystem functions such as productivity, biochemical cycles, its fauna, and stability (Scherer-Lorenzen *et al.* 2005).

The inclusion of Forests into BEF studies is limited by the space-scale and time-span at which their dynamic becomes relevant (Peh 2009). Until now, few long term experiments have been established, which would produce results under proper settings comparable to natural or semi-natural forest covers (http://www.treedivnet.ugent.be/index.html). Positive effects have been reported in early grown plantations, and have been explained in terms of differential growth of individuals in competition for light (Potvin & Dutilleul 2009).

Observational studies have tried to assess the relation between diversity and ecosystem functioning in forests. Although these studies allow the assessment on mature forests, the results are limited and can be confounded by environmental factors and their lack of design (species rich or species poor stands can be under represented and many species are not found naturally growing in monocultures). Results on mature forests are highly variable. For example, on natural or naturalized forests in Africa (Peh 2009), Europe (Vilà *et al*. 2003, Vilà *et al*. 2007, Pretzsch & Schuetze 2009, Jacob, Leuschner *et al*. 2010), North America (Long & Shaw 2010, Paquette & Messier 2011), Australia (Firn *et al*. 2007) have studied relations between diversity and ecosystem productivity, with negative (Firn *et al*. 2007, Jacob *et al*. 2010), neutral (Vilà *et al*. 2003, Peh 2009, Long & Shaw 2010) and positive relations (Vilà *et al*. 2007, Peh 2009, Pretzsch & Schuetze 2009, Paquette & Messier 2011). Most of the studies have been taken place in temperate and boreal forests (Hector *et al*. 2011) and more diverse forests from the subtropics and tropics are also underrepresented.

Forest area in Asia and China

Asian forest cover has experienced a strong dynamism during the last decades, as the countries develop and require more resources forests have been intensively exploited. Deforestation rates in Asia are only comparable with the ones in South America. However, the overall balance of forest cover doesn't reflect that pattern, as Asia is the continent with higher rate of afforestation also. China is the country with larger afforestation area worldwide. Although Chinese forest, especially in the south can be highly diverse, wood plantations are comparatively less diverse as most of the time only one species or very few are planted (Piotto *et al*. 2010, Paquette & Messier 2010).

Our study area is located in the subtropical Chinese forest. It is not only interesting within the framework of BEF because of the high diversity, but also as it is a relevant topic in the region. If

natural forests are reduced, and replaced by planted forests, ecological processes at a large scale, considering the size of china can be affected at local, regional and probably continental level.

Study area

Our study area is located in the borders of Zhejiang and Jiangxi provinces in southeast China and has a typical subtropical monsoon climate with an annual temperature of 15.1°C (maximum in July 38.1 °C) and a mean precipitation of about 1963.7 mm (Hu & Yu 2008, Bruelheide *et al.* 2011). The typical forests in the region are broadleaf mixed forests, with dominance of evergreen individuals. Up to now, 1462 seed plant species, of 684 genera and 149 families were recorded in the Gutianshan National Nature Reserve, which is one of our study sites. Over 250 species out of them are woody plants (Lou & Jin 2000, Bruelheide *et al*. 2011). Plant diversity of broad-leaved forest in southeast China determined the recognition of the region as a hotspot of phytodiversity (Barthlott *et al*. 2005).

Thesis outline

The central topic of this thesis is the diversity effects on aboveground productivity in forests. We ask if, as in grasslands, there is a positive diversity−productivity relationship in forest ecosystems. We evaluated the effect of diversity on biomass and growth in secondary subtropical forest stands (Chapter 1). We then investigated the relationship between diversity and density on seedling growth patterns (Chapter 2). Next we study if this relationship was consistent also on early growth of seedling communities and with different light conditions (Chapter 3). Finally, we study in more detail the mechanisms which explain the biodiversity−productivity relationship and how it is measured (Chapter 4).

In **Chapter 1**, we study the effect of tree diversity on stand growth. We did a comparative study by selecting twenty-seven forest stands with low, intermediate and high tree species richness,

crossed with young, intermediate and old stands. We measured every tree and calculated stand basal area and basal area increment over a two year period (2008-2010). We analyzed basal area and basal area increment of trees (≥ 10 cm DBH) and of younger cohort (≥ 3 cm and < 10 cm DBH) as a function of diversity (Species richness, functional and phylogenetic diversity) and successional stage. We found a strong diversity effect on both cohorts, which was defined by larger mean individual sizes and by higher densities in more diverse plots.

In **Chapter 2**, we explore the effect of species richness and density on sapling growth patterns. We tested for the effects of biomass allocation, crown architecture and branch demography in an experimental setting with mixtures up to four species (monocultures, 2-species mixtures and 4-species mixtures) and with three density levels (low-, intermediate- and high-density). Species richness enhances branch turnover, but growth was mainly determined by species identity. Competition for light seemed to govern crown architecture and branch demography. Intra-specific competition was stronger than inter-specific competition for two species.

In **Chapter 3**, we examine effect of species richness on sapling-community growth in different light conditions. We setup a garden experiment in which we planted three species pools (set of species) of four species, which were planted in monocultures (four communities), in 2-species mixtures (six communities) and 4-species mixtures (one community) in two light conditions (direct sunlight, shade). We found a positive effect of diversity (species richness), which was driven by the dominant species in each of the species pools. This effect was constant across the two light treatments, but its strength was affected by species specific survival and growth.

In **Chapter 4**, we explore the effect of species identity, species composition and functional distance on aboveground biomass on 2-species mixtures, how they relate to the mechanisms selection and complementarity effects and how diversity effects are measured. We assessed biomass in 18 2-species mixtures in two light conditions (out of the setup used in Chapter 3).

Functional dissimilarity and specific species composition (presence of dominant species in the mixture) determine effects on aboveground biomass, net effect and selection effect. Mechanistic diallel analysis proved to be a useful tool for assessing biodiversity effects, as measurements are independent of monoculture standards and thus are affected less by species which perform particularly different growing by itself.

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CHAPTER 1

Biodiversity promotes tree growth during succesion in subtropical forest

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Biodiversity Promotes Tree Growth during Succession in Subtropical Forest

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Abstract

Losses of plant species diversity can affect ecosystem functioning, with decreased primary productivity being the most frequently reported effect in experimental plant assemblages, including tree plantations. Less is known about the role of biodiversity in natural ecosystems, including forests, despite their importance for global biogeochemical cycling and climate. In general, experimental manipulations of tree diversity will take decades to yield final results. To date, biodiversity effects in natural forests therefore have only been reported from sample surveys or meta-analyses with plots not initially selected for diversity. We studied biomass and growth of subtropical forests stands in southeastern China. Taking advantage of variation in species recruitment during secondary succession, we adopted a comparative study design selecting forest plots to span a gradient in species richness. We repeatedly censored the stem diameter of two tree size cohorts, comprising 93 species belonging to 57 genera and 33 families. Tree size and growth were analyzed in dependence of species richness, the functional diversity of growth-related traits, and phylogenetic diversity, using both general linear and structural equation modeling. Successional age covaried with diversity, but differently so in the two size cohorts. Plot-level stem basal area and growth were positively related with species richness, while growth was negatively related to successional age. The productivity increase in species-rich, functionally and phylogenetically diverse plots was driven by both larger mean sizes and larger numbers of trees. The biodiversity effects we report exceed those from experimental studies, sample surveys and meta-analyses, suggesting that subtropical tree diversity is an important driver of forest productivity and re-growth after disturbance that supports the provision of ecological services by these ecosystems.

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Introduction

Tropical and subtropical forests range among the most productive ecosystems on Earth [1,2], significantly interacting with global biogeochemical cycles and regulating climate at the regional and global scale [3,4]. These ecosystems harbor a significant fraction of global plant diversity and are under increasing pressure from land-use change and intensification, associated fragmentation, as well as climate change [5] and pollution [6].

Experimental and theoretical evidence demonstrates that the functioning of many ecosystems depends on the diversity of their component species [7,8]. To date, most studies manipulating plant species diversity have been conducted in artificially established herbaceous communities, mostly in temperate climates, with comparably limited information on biodiversity-ecosystem functioning relationships in tree communities. Nevertheless, a number of recent survey studies and meta-analyses confirmed a generally positive correlation between species richness and primary productivity also in forests. Evidence bases on data originating from forest plantations and on survey studies in forest inventory plots. The plantations for which data are available often are characterized by the dominance of commercially important, fast-growing species, low stand ages and a lower structural complexity than the one found in natural or semi-natural forests. Therefore,

these two study types are complementary and may well reveal different biodiversity-productivity relationships.

Using meta-analysis, Piotto [9] analyzed an extensive data set compiled from a large number of tropical and temperate plantations. Tree species mixtures had higher productivity than monocultures, but no significant effect of tree species richness within mixtures was found. Vilà et al. [10] analyzed data from European forest plots differing in forest type and found a 24% increase in productivity in mixtures relative to monospecific stands. Both studies suggest that the productivity increase with diversity saturates at relatively low diversity levels. Paquette & Messier [11] studied productivity in forest inventory plots spanning a gradient from temperate to boreal, and found that diversity was an important determinant of productivity in boreal but not in temperate forests. Common to these studies, and complicating data interpretation, is the need to control for effects of drivers of tree diversity co-varying with species richness, in particular climate, soil fertility, and successional age, which is not always done [11]. Most sample surveys in natural and semi-natural forest were carried out in temperate or boreal forests characterized by rather low species diversity. For example, tree species richness averaged around two in the survey by Vilà et al. [10], with 51% of the plots being monocultures and another 42% being two or three species mixtures. The sample survey by Paquette & Messier [11] consisted of slightly more diverse plots (average of 3–5 species, depending on biome). An important conclusion emerging from the available literature is that data for natural subtropical and tropical forests is largely underrepresented or missing, despite their high species diversity and the importance of these ecosystems for the regulation of global processes.

Here, we adopted a comparative study design, deliberately selecting plots in a highly diverse subtropical secondary forest in south-east China to represent different levels of tree species richness and successional age. The comparative study approach has a higher power to detect effects of diversity, and is more likely to reveal causal relationships than sample surveys, but surprisingly has never been used to assess biodiversity–productivity relationships in forests. As dependent variables we measured the basal area and the two-year increase in basal area of all trees in the study plots. While effects of tree species richness are ultimately caused by functional differences among the species present in a community, this trait variation may not be fully captured by species numbers. We therefore also analyzed our data in relation to the diversity of a range of growth-related functional traits. To account for additional functional trait variation possibly reflected in phylogeny, we further included an index of phylogenetic diversity in our analyses. In this study, we successfully (1) tested for effects of tree species richness on productivity (2), compared the effect sizes we found to findings from other studies in forest but also grassland, and (3) tested whether functional or phylogenetic diversity would explain variation in the observed responses that is not explained by species richness.

Methods

Study site and experimental design

Field plots selected to represent different levels of tree species richness and successional age were established in Gutianshan National Nature Reserve, western Zhejian province, China (29°15' N, 118°07' E; mean annual temperature: 15.1°C, maximum: 38.1°C in July; mean annual precipitation: ~2000 mm; permission for this field study was granted by the Administration Bureau of the Gutianshan National Natural Reserve, Kaihua, China). Prior to its establishment in 1975, the ~81 km^2 site was managed as commercial forest planted with *Pinus massoniana* and *Cunninghamia lanceolata* [12]. Today, 1462 seed plant species belonging to 684 genera and 149 families are found in the reserve. The >250 tree species present include members with temperate (e.g. Fagaceae), subtropical (e.g. Anacardiaceae, Lauraceae) and tropical (e.g. Symplocaceae, Theaceae, Myrsinaceae) distribution, resulting in a diversity similar to the one of tropical forests [13,14].

Twenty-seven plots of 30 × 30 m area were deliberately selected to span factorial gradients in both tree species richness and successional age resulting from timber cutting by local communities. Average distance between plot pairs was ~3 km. The closest pair was 40 m apart, followed by 165 m and 243 m for the next-closest pairs. For each plot, we determined tree species richness from the inventory data we recorded (see below). Successional age was assigned to five age classes (<20, 20–40, 40–60, 60–80, or >80 years old) based on the age of the fifth-largest tree of each plot (determined from a stem core), because the precise date of the last logging event could generally not be determined. Our goal was to evenly cover the range in tree diversity and successional ages present at the site, although it was not possible to keep these two fixed, independent variables fully orthogonal to each other. In the further course of the study, two plots were lost due to (illegal) timber cutting. All analysis presented are therefore based on data from the remaining twenty-five plots.

We did not select plots randomly, because such a "sample survey" design would have resulted in a concentration of plots around mean tree species richness values, with a typically bell-shaped distribution. In sample surveys (and meta-analyses based on sample surveys), correlations between species richness and productivity are bi-directional relationships between two dependent variables. This problem can be alleviated by fixing one variable as independent variable at different levels that are similarly replicated, and then measuring the other variable as dependent variable. This approach is recommended e.g. in the classical statistical textbook by Snedecor & Cochran [15] who refer to this type of study as *comparative study* and rank it between *sample surveys* and *designed experiments* (with randomized treatments) with regard to the power to detect causal relationships between variables.

Tree size and growth

We tagged all tree individuals with a diameter at breast height of at least ten centimeters. The resulting "canopy" tree

cohort comprised of 1523 trees belonging to 66 species, 49 genera, and 29 families (Table S1 in File S1). In the central 10 × 10 m quadrat of each plot, all trees with a diameter of at least three but less than ten centimeters were also tagged. This "understory" tree cohort consisted of 672 individuals belonging to 58 species, 34 genera, and 19 families (Table S2 in File S1).

The diameter at breast height of all "canopy" and "understory" trees was determined in summer 2008 and again in 2010, using either permanently installed dendrometer bands or a metering tape. Tree diameters were converted into stem cross-sectional area (basal area). We further calculated basal area increments from 2008 to 2010 as a proxy of tree growth.

Functional diversity

We determined functional diversity sensu Petchey & Gaston [16], using a range of potentially growth-related species traits. For all species present in either the "canopy" or "understory" cohort, we recorded leaf seasonality (evergreen vs. deciduous), leaf habit (broadleaved vs. coniferous), specific leaf area (SLA), leaf carbon to nitrogen ratio (C:N), leaf size (dry weight of a typical mature leaf), the typical maximum height reached by mature individuals of the species, and the typical density of stem wood. Data were generally recorded on individuals sampled in Gutianshan National Nature Reserve [17,18]. For ten species, wood density was taken from the global wood density data base [19], re-scaling values based on the correlation of wood densities of species present in both data sets. All traits were normalized to zero mean and unit variance; twenty-one out of 282 values for leaf size, C:N, and SLA were missing and set to zero. Functional diversity was then calculated as total branch length of the functional-trait dendrogram (euclidian distances, complete linkage agglomeration), calculated for the particular set of species occurring in a plot (Fig. S1 in File S1).

Phylogenetic diversity

Phylogenetic diversity was calculated based on sequence information (*matK*, *rbcL* and the ITS region including the 5.8s gene) retrieved from GenBank or obtained using standard barcoding protocols. In brief, a phylogenetic tree including 440 woody species present at the field site was generated using a maximum likelihood (ML) method. Using the ML topology and branch lengths, an ultrametric tree was created by non-parametric rate smoothing, with 27 node ages constrained by published fossils and a fixed age of 125 million years for the crown node of the Eudicots. Data processing and the construction of the phylogenetic tree are reported in detail in Method S1 in File S1. Phylogenetic diversity was calculated as total branch length defined by the subset of species occurring in a plot (see Fig. S2 in File S1).

Evenness

Although plots were selected for species richness, we calculated species evenness based on the number of stems recorded for each species. We chose the evenness index $E_{1/D}=1/(DS)$, where D is Simpson's index of dominance and S species richness. We preferred $E_{1/D}$ over Shannon-Wiener-based indices because $E_{1/D}$ is independent of S [20].

Statistical analysis

Effects of tree diversity and successional age were tested by fitting multiple regression models with sequential sum of squares (lm function of R 2.15.0; http://www.r-project.org). Species richness effects were tested either independently of successional age (richness fitted before age), or after adjusting for effects of age (richness fitted after age). Since species richness was analyzed as continuous variable, effect sizes need to be reported based on an arbitrarily chosen change in species richness. Here, we report predicted changes in the analyzed variable for a hypothetical increases in species richness from ten to twenty species.

Plots had originally been selected by visually choosing plots with low, intermediate, or high diversity. The exact numbers of species was determined later. We therefore also repeated our analysis by fitting models with diversity as tree-level ordinal factor (each level containing approximately 1/3 of the plots), which better reflects the original plot selection procedure. Both analyses resulted in very similar results; we therefore only report data from the analyses including exact species richness.

Influences of site conditions were tested using the covariates elevation, slope aspect (north-south and east-west component), slope inclination, soil pH, soil moisture, and soil organic C and N. Since covariables often are collinear and will always explain some variation in the data set, even if just by chance, we normalized them (scaling to zero mean and unit variance) and aggregated these to orthogonal principle components. We then tested for effects of the (orthogonal) first two principal components by including these as covariates in our linear models.

We tested whether the number of trees found in the second census but not the first depended on species richness or successional age, i.e. whether non-random ingrowth of individuals into the cohort assessed occurred. Similarly, we tested for effects on the number of trees lost from the assessed size classes, i.e. whether non-random mortality or transitions from the understory to the canopy tree cohort occurred. These tests were conducted by fitting generalized linear models with log-link and Poisson error model accounting for overdispersion, if necessary (glm function of R).

Structural equation models including effects of tree diversity (latent variable defined by tree species richness, functional diversity, and phylogenetic diversity), successional age, and their indirect effects mediated by changes in tree density (i.e. the number of trees per plot) were fitted by generalized least squares (sem function, http://cran.r-project.org/web/packages/lavaan). Tree density was included as intermediate explanatory variable, because positive effects of biodiversity on plot-level cumulated size measures must, as a mathematical necessity, result from increases in the size of individuals, increases in their numbers, or from both.

Results

Richness effects on tree size and growth

In the "canopy" cohort (trees with diameter ≥ 10cm), total stem basal area per plot in 2008 increased linearly with tree species richness, which explained 45% of the observed

variation ($F_{1,22}$=26.9, P<0.001 in multiple regression with sequential sum of squares for richness followed by successional age; Figure 1a). Similarly, tree species richness explained a significant fraction of variation in the 2008–2010 increment in total stem basal area, a proxy for stand growth ($F_{1,22}$=7.7, P=0.01 in multiple regression with richness followed by successional age; Figure 1b). Per 10 extra species, these effects correspond to an additional stem basal area of 17.8±4.1 m^2/ha, or a +82% increase when doubling species number from 10 to 20. For the 2008–2010 growth of stem basal area, these numbers correspond to 0.46±0.17 m^2/ha, equivalent to a +45% change when increasing tree species number from 10 to 20. Despite the partial confounding of measured tree species richness and successional age (Pearson's product moment correlation, r=0.60, P<0.01), effects of tree species richness remained significant after adjusting for successional age ($F_{1,22}$=4.5, P=0.04 for total stem basal area; $F_{1,22}$=9.8, P<0.01 for increment of total stem basal area; richness fitted after successional age in multiple regression). These adjusted effects correspond to a +44% increase in stem basal area and a +62% increase in stem basal area increment when increasing species numbers from 10 to 20.

The same positive relationship between tree species richness and dependent variables was also found for "understory" trees (3cm ≤ diameter < 10cm; Figures 1c, d). In contrast to the "canopy" tree cohort, tree species richness and successional age were marginally significantly negatively correlated for understory trees (r=–0.34, P=0.1). Species richness of understory trees explained a significant fraction of their total stem basal area in 2008 ($F_{1,22}$=20.2, P<0.001) and their increment in total stem basal area from 2008–2010 ($F_{1,22}$=1.4, P<0.001). These effects correspond to an increase in basal area of 9.55±2.37 m^2/ha (+129%) and an increase in basal area growth of 1.22±0.38 m^2/ha (+111%) when doubling understory species numbers from 10 to 20. These effects remained significant ($F_{1,22}$=11.3, P<0.01 and $F_{1,22}$=6.3, P=0.02) when first adjusting for successional age and correspond to a +103% increase in stem basal area and a +75% increase in stem basal area growth when doubling understory species numbers from 10 to 20.

In our study, species richness and evenness were significantly negatively correlated, both for the canopy (r=-0.5, P=0.01) and the understory tree cohort (r=-0.57, P=0.003). As a consequence, basal area and basal area increment were significantly negatively related to evenness for both size cohorts (P=0.04 for canopy tree basal area increase, P<0.001 for all other cases).

The wood density of the species recorded in our census spanned a factor of approximately two. If substantial shifts in wood density of the species present would occur with diversity, this would bias basal area as an indicator of productivity. To explore this possibility, we repeated our multiple regression analysis, this time scaling basal area with the wood density of the species. Results remained essentially the same and are therefore not reported here. Note, however, that this analysis is not properly replicated since wood density was not determined on a per-plot basis but considered a constant property of the species, which clearly is simplistic.

When covariates describing plot characteristics were included in the analysis (aggregated as principle components), effects of species richness remained significant in all cases. These covariates explained virtually no variance in the data (on average less than 1%) except for basal area of the canopy cohort (7% and 17%).

Functional diversity, phylogenetic diversity, and stand density

Structural equation models including diversity as a latent variable combining species richness, functional diversity, and phylogenetic diversity indicated that successionally older stands had higher total stem basal area and reduced growth of canopy trees (Figure 2a, b; path coefficients linking AGE with BA and ΔBA, respectively). In contrast, diversity increased total stem basal area (Figure 2a), with a substantial component of the effect being indirect via increases in the number of trees, i.e. in stand density. Diversity also increased total stem basal area growth (Figure 2b).

Successional age exerted little influence on understory trees. However, diversity also increased basal area and basal area increments in this cohort, with effects being mediated primarily by increases in number of trees per plot rather than by enhanced individual growth (Figure 2c, d).

Relative growth rates of individual trees decreased in the canopy cohort (P<0.01, linear model, Figure 3a). Structural equation modeling suggested that this effect was driven indirectly by increased number of trees at high diversity (i.e. increased stand density), which resulted in reduced individual growth rates (Figure 3b). In the understory cohort, positive effects of diversity on individual growth rates were cancelled by negative effect via increased density, resulting in the absence of an overall effect (Figure 3c,d).

Transitions between size cohorts

Using general linear models with binomial error distribution, no effects of species richness or successional age on the in-growth into the canopy tree cohort were found. Similarly, we did not record statistically significant losses from the censored cohorts. Also, the number of additional trees found in the second census and the number of trees lost between censuses was small (8.5 and 2.3 individuals per plot, respectively, in the canopy cohort; corresponding numbers were 1.7 and 1.4 in the understory cohort).

Discussion

Our results indicate strong, positive effects of tree species richness on stand total basal area and growth. These effects were primarily mediated by increased individual growth of the bigger trees reaching the canopy, and by an increased density of individuals in the smaller understory trees. Functional and phylogenetic diversity were strongly positively correlated to species richness, and did not explain substantial variation in addition to the effects explained by species numbers.

Stand growth as assessed by increment of total stem basal area can underestimate woody biomass accumulation due to allometric scaling. It is therefore even more remarkable that the

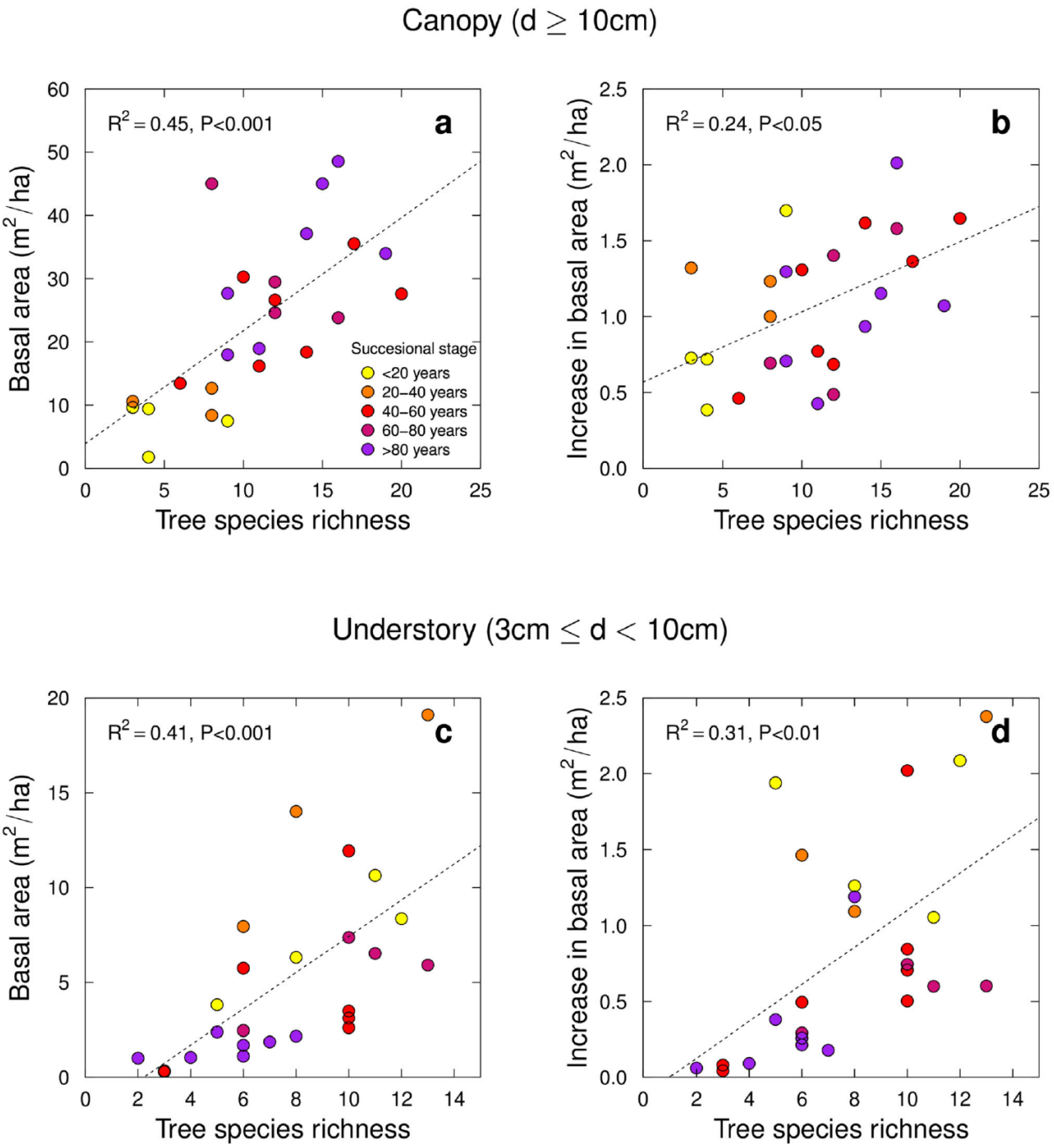

Figure 1. Total stem basal area in 2008 (a, c) and increment of total stem basal area from 2008 to 2010 (b, d) as functions of tree species richness and successional age of the study plots. Growth was assessed separately for canopy trees with a diameter at breast height (d) of 10 cm or larger (a, b) and for understory trees with d between 3 and 10 cm (c, d).

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diversity effects we report here are larger than effects reported for many herbaceous and woody ecosystems. Normalized effect sizes Zr ranged from 0.44–0.81 for total stem basal area and from 0.51–0.63 for increment of total stem basal area in our study, depending on whether effects of successional age were adjusted prior to testing the effect of species richness and whether the canopy or understory tree cohort was considered; these effect sizes appear exceptionally high when compared to

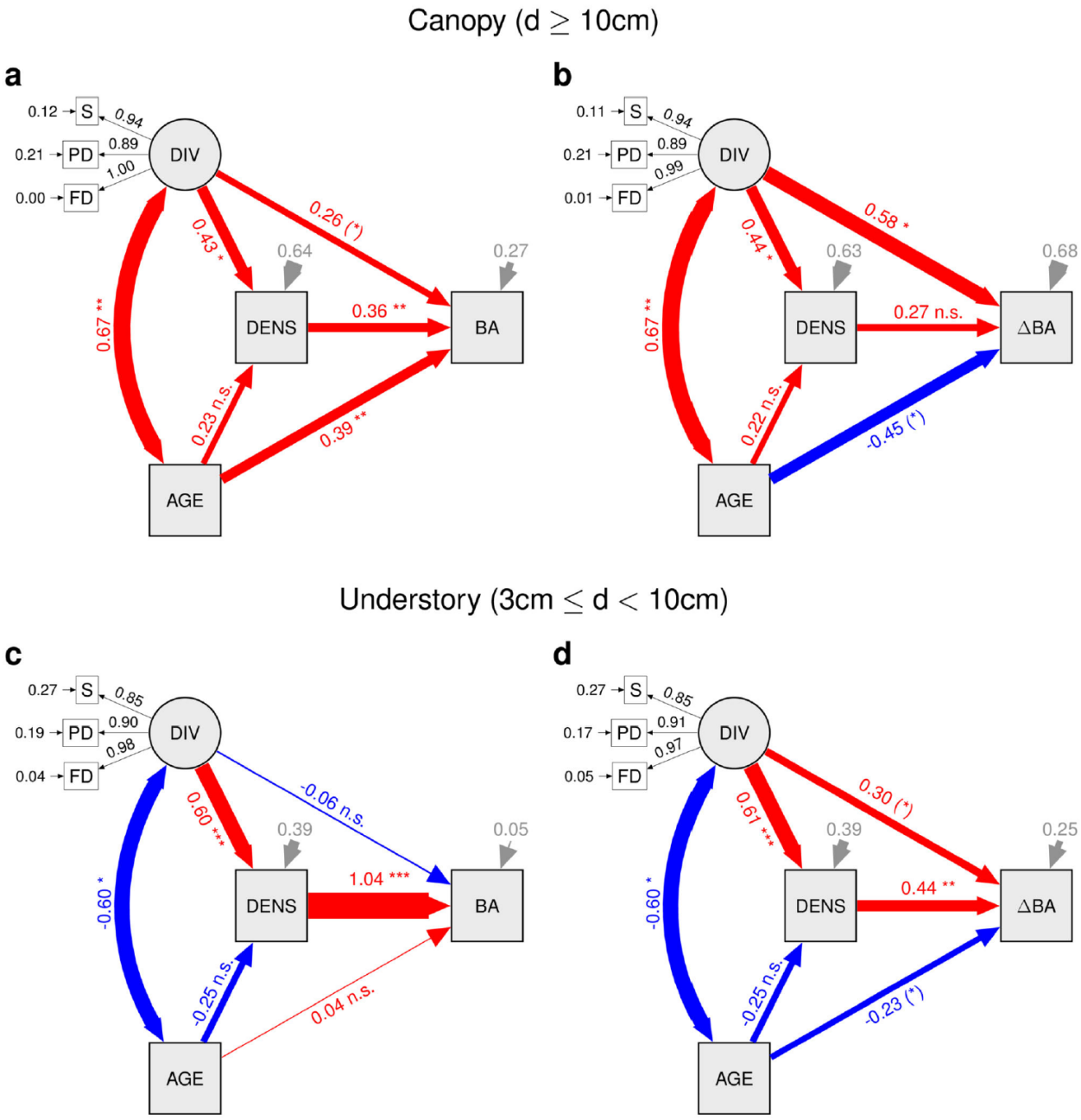

Figure 2. Structural equation models fitting total stem basal area in 2008 (a, c) and increment of total stem basal area from 2008 to 2010 (b, d) in dependence of successional age, tree diversity, and tree stem density. Path diagrams indicate effects of tree species diversity on the two dependent variables, either directly or indirectly via increases in tree density. The diagrams show standardized path coefficients (red: positive; blue: negative) and associated statistical significances (*** P<0.001; ** P<0.01; * P<0.05; (*) P<0.1). Variable abbreviations: S = species richness, PD = phylogenetic diversity, FD = functional diversity, DIV = diversity (latent variable related to previous three), AGE = successional age, DENS = tree density, BA = total stem basal area, ΔBA = increment of total stem basal area.

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a recent meta-analysis [8,21] in which only few field studies showed similar or higher Zr for primary production; these generally were the studies in which biodiversity effects were strongly driven by legume responses [22]. The available meta-

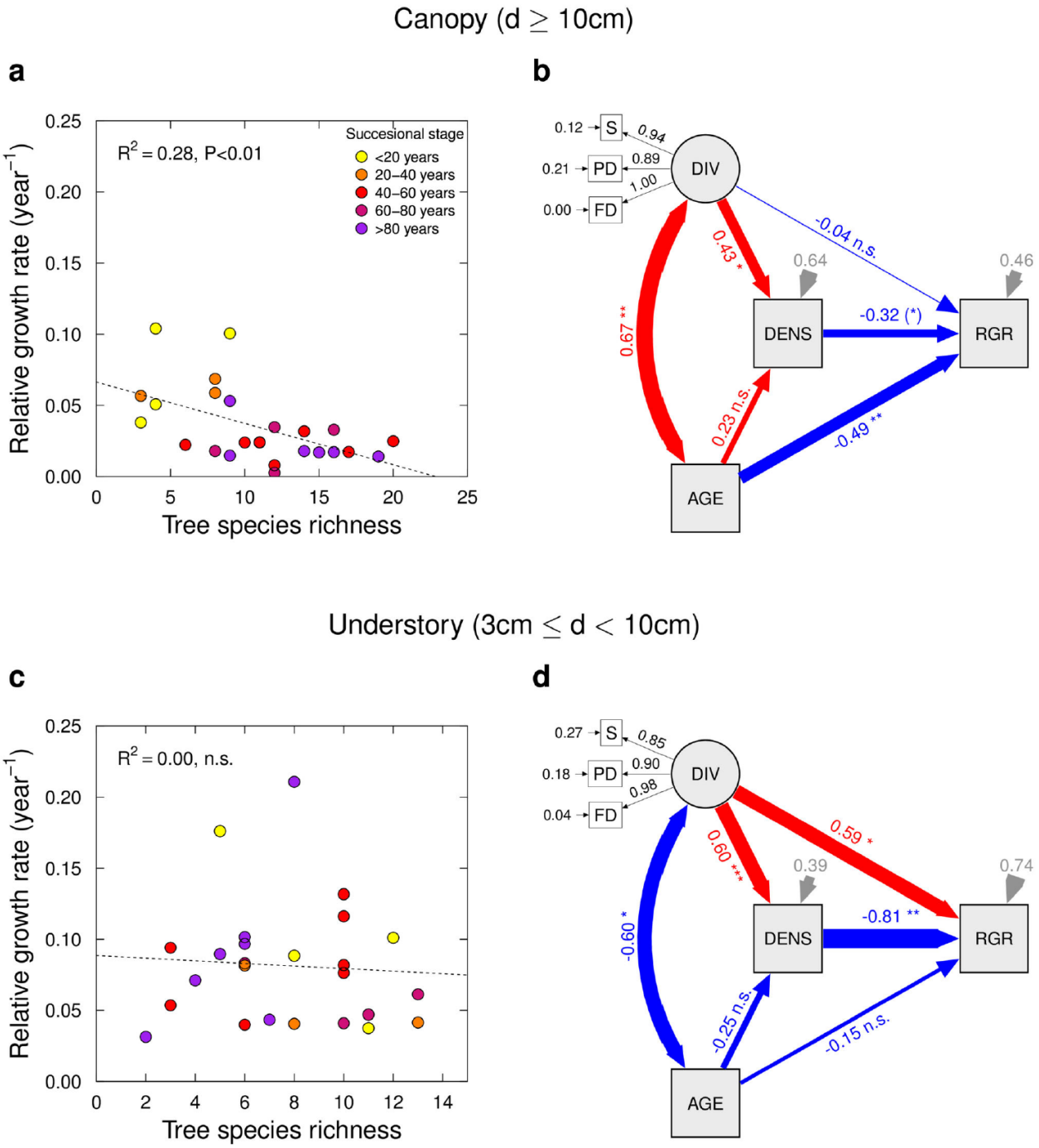

Figure 3. Relative growth rate of individual stem basal area (RGR, 2008–2010 period) in dependence of successional age, tree species richness, and tree stem density. In the canopy tree (d>10 cm) cohort, RGR declines with diversity (a) due to its correlation with successional age (b; path from DIV via AGE to RGR); in the understory (3 cm<d<10 cm) cohort, a positive direct and negative indirect (via density) effect of species richness on RGR balance each other out (c, d). The diagram shows standardized path coefficients (red: positive; blue: negative) and associated statistical significances (*** P<0.001; ** P<0.01; * P<0.05; (*) P<0.1). Variable abbreviations: S = species richness, PD = phylogenetic diversity, FD = functional diversity, DIV = diversity (latent variable related to previous three), AGE = successional age, DENS = tree density, BA = total stem basal area, ΔBA = increment of total stem basal area.

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analysis comparing forest polycultures to monocultures also report much lower effects; for example, Piotto [9] reports a cumulated effect size of d+=0.31, corresponding to Zr≈0.32, and Zhang et al. [23] reports a 24% higher productivity in mixtures, with a saturation of the productivity at a diversity of about six species. Our findings are thus in line with recent reports [24] indicating that biodiversity contributions to ecosystem change are similarly important as effects of other global change drivers, including eutrophication and atmospheric CO_2 increases.

Our findings contrast with the view that biodiversity–ecosystem functioning relationships are weaker in natural than in experimental systems [8,25], or even absent due to high species similarity resulting from strong environmental filtering [26]. The positive relation between richness and productivity we report is opposite to a trend often observed in sample surveys along environmental gradients [15] in which high productivity coincides with low species diversity [27,28]. Such a negative correlation between biodiversity and productivity has often been attributed to competitive exclusion under increased productivity, and to dissimilarities in local species pool composition, i.e. β-diversity [29]. In our study, the strong positive correlation between biodiversity and productivity indicates that these factors were not at play at the spatial scale covered, or that these were of subordinate importance. Indeed, it is conceivable that biodiversity effects are even stronger in natural communities than in randomly assembled experimental communities [30], potentially due to pronounced species differences resulting from processes limiting similarity (e.g. competition for the same ressources, or effects of shared pathogens) [31,32].

Interestingly, density-mediated biodiversity effects on growth have also been found in an experimental study with herbaceous communities [33], with individual sizes orders of magnitude lower than for trees. The larger number of individuals we found in more diverse plots possibly results from complementarity among species, i.e. from reduced competition between individuals due to niche differentiation and facilitation. Similar effects have been found in experimental herbaceous communities [33]. While the relationship between density and diversity is potentially bi-directional, structural equation models that do not allow effects of diversity mediated via density (and which therefore may be overly conservative) largely confirmed our findings (Figure S3 in File S1).

Species richness and evenness were significantly negatively correlated in our experimental plots. Such a relation has also been found in designed experiments with artificially established herbaceous systems [34]. This inverse relation between richness and evenness is at least in part the result of the typical rank-abundance relationships found in natural communities, i.e. individual numbers decline rapidly with rank, leaving only few dominant and subdominant species. Under these conditions, increasing diversity essentially results in the addition of rare species, and evenness therefore declines.

Controlling for factors other than diversity is crucial in non-experimental studies to rule out confounding with these other drivers. Plant species richness in subtropical forest communities (α-diversity) is determined by many factors, including habitat properties. In a 24 ha permanent forest plot nearby our study site, spatial structuring of habitat accounted for approximately one quarter of the variation in diversity between subplots (β-diversity) [13]. Nevertheless, at our study site the measured topographic and soil variables did not explain the observed diversity effects; also, a previous study of community structure in the same plots had shown that these covariates were unrelated to tree and shrub species richness [12]. Topography in Gutianshan Reserve is very rugged, evidenced in a broad variation in slope among our experimental plots; specific habitat properties may therefore scale with horizontally-projected plot area rather than with surface area. However, when we repeated the analyses using projected plot area, we obtained virtually identical results as when using surface area as reference.

Overall, our study suggests that tree species richness is an important factor enhancing community-level regrowth during secondary succession, contributing to resilience after disturbance. Our results further indicate that high tree species richness in these forests contributes to sustained growth even in old stands, either directly or indirectly through increased stand densities. Faster regrowth at high diversity may have important implications for a range of ecosystem services including erosion control and carbon storage. The rugged terrain at the field site, combined with high-intensity precipitation, renders slopes particularly susceptible to erosion and deterioration. Atmospheric source-sink balancing indicates a partly unresolved residual terrestrial CO_2 sink [35]. Recent evidence indicates that secondary vegetation regrowth after wood harvesting contributes to this sink [36]. Our results hint at the possibility that the strength of this sink might depend on the biodiversity of forest stands.

Supporting Information

File S1. (PDF)

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Author Contributions

Conceived and designed the experiments: BS HB KM. Performed the experiments: MB XC. Analyzed the data: MB PAN BS. Contributed reagents/materials/analysis tools: SM. Wrote the manuscript: MB BS PAN HB XC AH KM SM ZT.

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CHAPTER 2

Mechanisms promoting tree species co-existence: Experimental evidence with saplings of subtropical forest ecosystems of China

Anne C. Lang, Werner Härdtle, Martin Baruffol, Martin Böhnke, Helge Bruelheide, Bernhard Schmid, Henrik von Wehrden, Goddert von Oheimb (2012)

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Abstract

Questions: The maintenance of a diverse sapling pool is of particular importance for the regeneration and persistance of species-rich forest ecosystems. However, the mechanisms of co-existence of saplings have rarely been studied experimentally. Do species richness, species composition, species identity and stand density affect the co-existence, growth patterns and crown architecture of tree saplings?

Location: Jiangxi Province, southeast China.

Methods: In a field experiment, we manipulated the local neighbourhood of saplings of four early-successional subtropical species (*Schima superba*, *Elaeocarpus decipiens*, *Quercus serrata* and *Castanea henryi*) with regard to species richness (one, two and four species), species composition (monocultures, six-two-species combinations and one-four-species combination) and stand density (low, intermediate and high). We tested for treatment effects and impact of species identity on growth variables, biomass allocation, crown architectural traits and branch demography.

Results: Species richness was a poor predictor of all response variables, but enhanced pruning and branch turnover. In contrast, species composition proved to be of great importance for growth, biomass allocation, crown architecture and branch demography. Local neighbourhood interactions of saplings were characterized by complementary or facilitative, as well as by competitive mechanisms. Intra-specific competition was higher than inter-specific competition for two species (*C. henryi*, *Q. serrata*) depending on the respective species combination. To a high degree, the competitive ability of species can be explained by species identity. Competition for light likely played a major role in our experiment, as evidenced by the strong response of crown architecture and branch demography to the manipulated predictor variables.

Conclusions: Effects of species composition and species identity on growth rates and crown architecture variables of tree saplings point to niche separation as a mechanism of species co-existence, while effects of species richness were not yet prominent at the sapling life stage.

Introduction

The question as to which mechanisms maintain and promote species co-existence has become increasingly important in light of biodiversity loss and species extinction (Barot 2004; Hillebrand & Matthiessen 2009). Two theories play a key role in the current discussion on plant species co-existence: neutral theory and niche theory. According to neutral theory, functional equivalence (i.e. co-occurring species do not have to be different in rates of growth, dispersal or speciation), together with stochastic events, is a sufficient explanation for species co-existence

(Hubbell 2005; Rosindell et al. 2011). Niche theory, by contrast, implies that co-existence is explained by inter-specific differentiation in response to exploitative competition for environmentally limiting resources (DeClerck et al. 2005; Kraft et al. 2008) or in response to species-specific pathogens (Petermann et al. 2008; more general: Loreau & Hector 2001; Silvertown 2004; Levine & HilleRisLambers 2009). Niche partitioning may occur in space, in time or with regard to the quality of resources. As a result, in species combinations resources may be used in a complementary and more efficient way than in monocultures, and inter-specific competition is reduced compared to intra-specific competition (Kahmen et al. 2006).

For trees, the most important above-ground resource is light (Denslow 1987; Canham et al. 1994). Since light-harvesting efficiency is significantly affected by biomass allocation to leaves, foliage distribution and branching frequency (Niinemets 2010), the separation in niche space with regard to light harvesting should be evidenced by species-specific growth patterns, biomass allocation or plant architecture. In addition to abiotic factors, competitive interactions strongly influence individual tree growth. In particular, crown dimensions and architecture are known to respond sensitively to local neighbourhood interactions (Biging & Dobbertin 1992; Getzin et al. 2008; Schröter et al. 2011). However, to explain the spatial development of crowns in detail, information on single branches of individual trees is needed, since the process of crown expansion depends on the spatial development of branches and branch demography, which in turn is affected by local neighbourhood interactions (Franco 1986; Stoll & Schmid 1998; Sumida et al. 2002).

In this study, we experimentally analyse mechanisms of species co-existence of individual trees at the sapling stage, making use of the local neighbourhood approach (Pretzsch 2009). The maintenance of a diverse sapling pool is important to ensure the regeneration and persistence of species-rich forests (Bruelheide et al. 2011). We refer to tree saplings as young tree individuals that have survived the critical seedling phase and whose local neighbourhood is characterized by strong competition caused by a high density of similar-aged individuals. Important factors of this local neighbourhood which might affect the individual performance of tree saplings are species richness and species composition, species identity, stand density and the size of the tree saplings. The focus on individual tree growth patterns, biomass allocation and architectural traits is particularly promising in woody species, because these species have easily identifiable, large individuals with biomass accumulation in long-lasting structures.

We planted saplings of four early-successional subtropical species in monoculture as well as in two- and four-species combinations. In order to determine whether niche separation is the mechanism that enables the co-existence of these species in an early stage of their life, we tested for species richness, species composition and species identity, as well as for density and initial diameter size effects. Specifically, we tested the following hypotheses:

(H1) Species richness of the local neighbourhood affects the growth and morphology of saplings.

(H2) Species composition of the local neighbourhood affects growth and morphology of saplings.

(H3) Species identity of the target sapling is an important predictor of its growth and morphology.

(H4) Density affects growth and morphology of saplings.

Methods

Study area and experimental design

Our experiment was set up near Xingangshan, Jiangxi Province, southeast China (29°06′33″N, 117°55′24″E). The study area is characterized by a subtropical monsoon climate with an average annual precipitation of approximately 2000 mm and a mean temperature of 15.1 °C. The natural vegetation is a subtropical broad-leaved forest with dominance in abundance of evergreen species (Bruelheide et al. 2011). Nevertheless, the number of occurring deciduous and evergreen species is almost balanced (Lou & Jin 2000). The subtropical broad-leaved forest ecosystems of southeast China represent a global hotspot of phytodiversity (Barthlott et al. 2005).

The experimental area was a former agricultural field, which was ploughed, harrowed and divided into four blocks prior to setting up the experiment in March 2009. Four highly abundant, early-successional species were chosen for the experiment: *Schima superba* Gardn. et Champ., *Elaeocarpus decipiens* Hemsley (evergreen), *Quercus serrata* Murray and *Castanea henryi* (Skan) Rehd. et Wils. (deciduous) (Yu et al. 2001). We manipulated species richness and species composition of tree saplings on plots of 1 m² in size. Three plot-related species richness levels were established: monocultures, two-species combinations and four-species combinations. The four monocultures of each species, all six possible two-species combinations, and one four-species combination made a total of 11 species compositions. In addition to enabling analysis of species richness effects, the comparison of all possible species combinations also makes it possible to identify the effects of intra-specific vs. inter-specific competition (Massey et al. 2006), as well as competitive dominance of specific species. Species identity was treated as another predictor variable in the experiment. Finally, the species richness and species composition treatments were fully crossed with a density treatment. The low-density

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treatment comprised only one individual per plot, whereas the experimental plots with high and intermediate density each contained 16 individuals, planted in an array of four by four. Planting distances between saplings in the high- and intermediate-density treatment were 15 and 25 cm, respectively. The high, intermediate and low densities in this experiment refer to 44 000, 25 000 and 10 000 saplings per ha, respectively. In the nearby Gutianshan Nature Reserve, densities of 16 000 individuals per ha were found in an early successional secondary forest stand (<20 yr; Bruelheide et al. 2011). In the species combinations, each species was represented by the same number of individuals in both the peripheral rows (i.e. 12 individuals) as well as in the centre (i.e. four individuals). To avoid edge effects, all analyses were performed using the four central individuals. All treatment combinations were replicated four times, once in each of the four blocks. The total number of plots was 132 (11 species compositions x two densities (high, intermediate) × four blocks + 11 low-density plots spread over four blocks × four species = 88 + 44 plots). All treatment combinations were randomly assigned to plots within blocks. The experiment was run until September 2010, when destructive harvest took place. Individuals of the intermediate density treatment of one block were harvested in July 2010.

Field measurements

Sapling mortality

Over the course of the experiment, 223 out of 1452 saplings died (15.4%; number of dead saplings per species: *C. henryi* 92, *S. superba* 95, *Q. serrata* 18, *E. decipiens* 18). Since 96% of these dead individuals died during the first growing season (March to October 2009), post-planting stress was assumed to be the main reason for sapling mortality. Consequently, only data of saplings that survived this phase of establishment were incorporated in the analyses.

Sapling growth

Total height of saplings (i.e. length from ground to apical meristem) was measured in November 2009 and September 2010. Stem diameter at base height was measured 5 cm above ground in N-S and E-W direction with calipers, and the mean value was used in the analyses. The position of the diameter measurements was marked permanently with white paint. Measurements were taken in March 2009 (initial stem diameter), November 2009 and September 2010. Growth rates of absolute height and diameter were calculated as: [value (September 2010) – value (November 2009)]/11.

Above-ground biomass

To analyse biomass allocation patterns with regard to stratification (i.e. height layers) and to different constituents (stem, branches and leaves), the four central individuals per plot were harvested in September 2010 in 50-cm strata starting from ground level. Saplings were divided into stem, branches and leaves for each stratum. Biomass was dried at 70 °C for 48 h and weighed to 0.01 g precision. Biomass data were logarithmically transformed prior to analyses.

To analyse the vertical above-ground biomass distribution, we calculated the cumulative biomass fraction *C*, i.e. the proportion of cumulative above-ground biomass, summed from ground level to the height strata *hs* (50, 100, 150, 200, 250 cm). For each individual we fitted the coefficient of vertical biomass distribution as the linear regression coefficient β of *C* over *hs* (see Jackson et al. 1996; Vonlanthen et al. 2010). The coefficient of vertical biomass distribution indicates the steepness of declining *C* with increasing *hs*. Higher coefficient values, in turn, indicate biomass more evenly distributed over the total height of the tree.

Crown architecture

All crown architectural parameters were determined in June and September 2010. A branch was defined as a primary furcation longer than 1 cm. The height of the first branch was measured, and crown length was calculated as the difference between total sapling height and height of the first branch. The length of the first and the longest branch was measured as the distance from the stem to the longest tip of the respective branch.

Branch demography

Branches were counted bi-monthly during winter 2009/2010 (November, January, March) and monthly from April to June 2010 and in September 2010. Branch turnover and pruning are interpreted as a measure of adaption ability to changes in neighbourhood conditions over time. Branch turnover was calculated as the sum of all changes in branch number (no matter whether positive or negative) from November 2009 to June 2010. Pruning was defined as the sum of all negative changes in branch number (November 2009 to June 2010) and describes the dieoff of branches over time.

Statistical analyses

First, the complete data set was used to test for (H1) by fitting mixed effects models (Model 1) including species richness and density as factorial variables and the initial diameter as fixed effect. The initial diameter was used to

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account for differences in size at the beginning of the experiment. Second, all two-species combinations were analysed for species composition (H2). Mixed effects models (Model 2a) were fitted using species composition, density and initial diameter as fixed effects. The analyses with Model 2b were performed for the high-density treatment data divided by species to exclude density effects and to test for composition effects on the individual level of each species. Species composition in Model 2a referred to the mean over all individuals of a given species composition, whereas in Model 2b species composition referred to the mean of individuals of a specific species within a given species composition. Model 2b contained species composition and initial diameter as fixed effects. Third, mixed effects models (Model 3) for all monocultures were calculated to test (H3). They were fitted by the predictor variables species identity, density and initial diameter as fixed effects.

Random effects for all models were plot nested in block. Model simplification was performed by step-wise backward selection of fixed factors, removing the least significant variables until only significant predictory variables remained ($P < 0.05$). Since all density treatments were included in the analyses of Models 1, 2a and 3, the complete data from the June 2010 measurements was used to ensure a balanced data set. Model residuals did not show violation of modelling assumptions (normality and homogeneity of variances). The significant categorical variables were further examined by a Tukey *post-hoc* test. For the sake of clarity and more comprehensive analyses, the models presented here did not account for the presence and absence of species (for these models Appendix S1). We conducted a test for a phylogenetic signal (K statistics) in the observed growth and crown architectural traits. Although the K values for crown length and branch biomass were close to one, none of the values were significant, and we did not consider phylogeny in the statistical analyses (Appendix S2). In addition, we calculated Pearson correlation coefficients between height and diameter growth rates and crown architectural variables. If not indicated otherwise, values are given as mean with standard deviation.

All statistical analyses were performed using R 2.12. (R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria) using the packages nlme for the analyses of mixed effects models, multcomp for *post-hoc* Tukey tests and picante for the K statistics.

Results

Height and diameter increment

The mean sapling height at the time of planting was 33 cm ± 13 cm, compared to a mean height of 124 cm ± 39 cm at the end of the experiment. *S. superba* (6.74 ± 2.17 cm month^{-1}) had the highest mean absolute height growth rate, followed by *E. decipiens* (6.31 ± 2.27 cm month^{-1}), *Q. serrata* (5.57 ± 2.34 cm month^{-1}) and *C. henryi* (3.63 ± 2.67 cm month^{-1}). Species richness had no significant impact on the absolute height growth rate of saplings. However, species composition significantly affected absolute growth rates ($P = 0.03$). Model 2b revealed that the height growth rate of *C. henryi* ($P = 0.019$) and *Q. serrata* ($P = 0.046$) individuals was affected by species composition. Individuals of both species were significantly higher in combination with *E. decipiens* compared to monocultures. The absolute height growth rate was also influenced by species identity ($P < 0.001$). Neither density nor the initial stem diameter of saplings affected height growth.

The mean absolute diameter growth rates per month were: *E. decipiens* (0.7 ± 0.5 mm) > *S. superba* (0.6 ± 0.3 mm) >*Q. serrata* (0.5 ± 0.3 mm) >*C. henryi* (0.3 ± 0.3 mm). Absolute diameter growth rates were neither affected by species richness nor by species composition. However, species identity was a highly significant predictor of diameter growth ($P = 0.008$). The diameter growth rate of *C. henryi* was significantly lower than that of *S. superba* and *E. decipiens* ($P < 0.05$). In addition, density had a significant influence on absolute diameter growth rate ($P < 0.001$). The diameter growth of saplings was significantly enhanced in the low-density treatment compared to both the intermediate- and high-density treatment ($P < 0.001$). In contrast, the initial stem diameter had no significant effect on diameter growth.

Both absolute height and diameter growth rates were positively correlated with crown length (Pearson correlation coefficient, $r = 0.84/0.50$, respectively), the length of the longest branch ($r = 0.40/0.51$) and the number of branches ($r = 0.49/0.45$).

Above-ground biomass

Model 1 revealed no significant effect of species richness on above-ground biomass or on the coefficient of vertical biomass distribution. Species composition, in contrast, significantly influenced biomass increment ($P = 0.009$) and allocation to different constituents ($P < 0.01$). Results of Model 2b showed that *C. henryi* individuals accumulated significantly more biomass in combination with *E. decipiens* than in the monoculture ($P < 0.001$) and in combination with *S. superba* ($P = 0.023$; Fig. 1a). The biomass of leaves of *C. henryi* individuals was significantly lower in monocultures than in combination with *E. decipiens* ($P = 0.005$) or in the four species combination ($P = 0.025$; Fig. 1b). Similar to *C. henryi*, the stem and total biomass of *Q. serrata* individuals was higher in combination with *E. decipiens* than in

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monoculture ($P < 0.01$) and in combination with *C. henryi* ($P < 0.05$; Fig. 1c, d). Species identity was a significant predictor of all biomass-related variables (all $P < 0.001$). In general, results of post-hoc Tukey tests revealed that the biomass of all constituents of *C. henyri* was significantly lower than that of the other species (Table 1).

Stratum-related biomass allocation patterns of different constituents proved to be quite stable over density treatments for each species (Fig. 2). Species identity effects were evident for the coefficient of vertical biomass distribution ($P < 0.001$). Increasing density had negative effects on all biomass constituents ($P < 0.05$), whereas no density effects on the vertical biomass distribution were found. Regarding the total above-ground productivity within the low-density treatment, the four species ranked as follows: *S. superba* (157.2 ± 134.7 g) >*E. decipiens* (135.2 ± 145.99 g) >*Q. serrata* (97.0 ± 92.3 g) >*C. henryi* (42.0 ± 43.4 g).

Crown architecture

Species richness had no effect on crown architecture, whereas species composition proved to be a significant predictor for all crown architectural variables ($P < 0.05$ for all variabels). Model 2b results show that species composition had a significant effect on crown length of *C. henryi* and *Q. serrata* and on the length of the longest branch of *S. superba*. The crown length of *C. henryi* was significantly enhanced when growing with *E. decipiens* compared to both the monoculture and the combinations *C. henryi–S. superba* and *C. henryi–Q. serrata* ($P < 0.05$). Moreover,

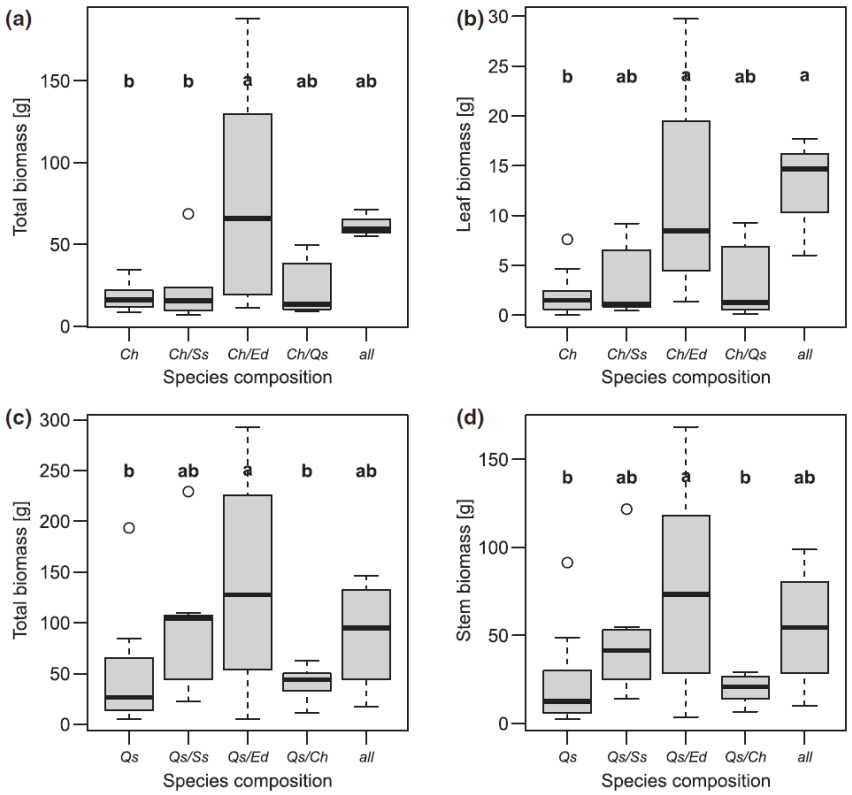

Fig. 1. Boxplots of the individual total biomass (**a**) and leaf biomass (**b**) of *Castanea henryi*, and of total biomass (**c**) and stem biomass (**d**) of *Quercus serrata* in the different species combinations. Significances of *post-hoc* Tukey tests ($P < 0.05$) of the explanatory variable 'species composition' tested by Models 2b are indicated by different letters. Species codes: Ch: *C. henryi*; Ed: *E. decipiens*; Qs: *Q. serrata*; Ss: *S. superba*.

Table 1. Mean values of above-ground biomass allocation to different constituents (dry weight per plant [g] and standard deviations) for the four species.

Constituents	*Castanea henryi*	*Elaeocarpus decipiens*	*Quercus serrata*	*Schima superba*
Total	13.9 ± 10.8^{a}	34.5 ± 33.6^{b}	37.8 ± 25.6^{b}	56.7 ± 33.7^{b}
Stem	20.2 ± 22.8^{a}	69.9 ± 68.6^{b}	47.9 ± 45.8^{b}	57.3 ± 42.8^{b}
Branches	13.6 ± 14.6^{a}	44.7 ± 62.2^{b}	18.5 ± 22.2^{a}	32.5 ± 36.3^{b}
Leaves	8.2 ± 11.0^{a}	20.6 ± 30.3^{ab}	30.1 ± 28.0^{b}	67.4 ± 61.9^{c}

Different letters show significant *post-hoc* Tukey results ($P < 0.05$).

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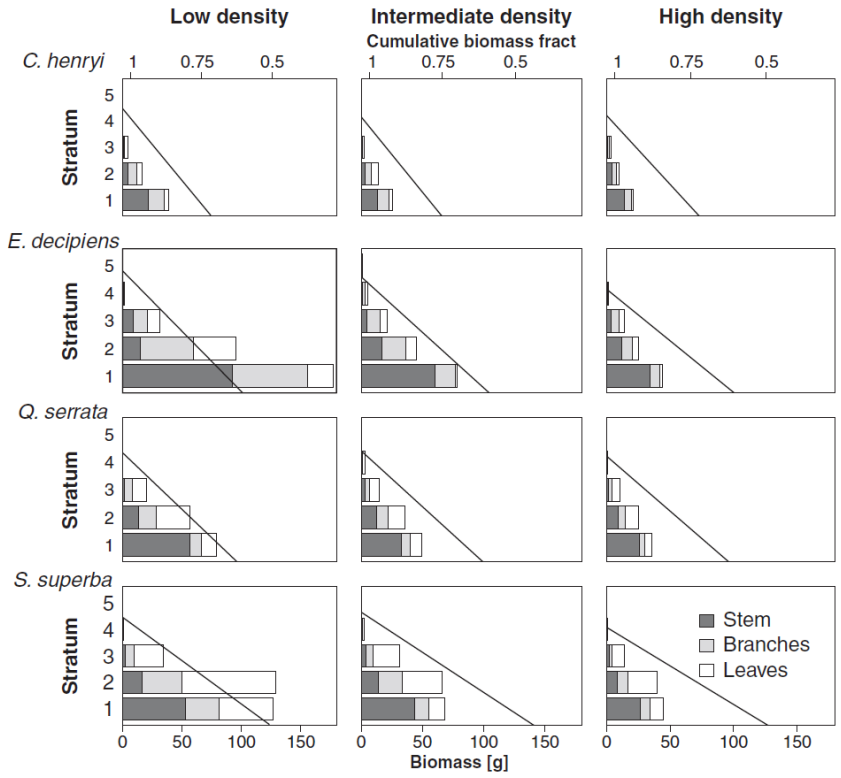

Fig. 2. Allocation patterns of the biomass constituents (stem, branches, leaves) per individual over different strata. Mean biomass values per strata are shown for species of the different density treatments (bar plots). Each stratum comprises 50 cm in height. The black line represents the mean coefficient of vertical biomass distribution for the respective species and density treatment.

the crown length of *C. henryi* was higher in the four-species combination compared to the monoculture ($P < 0.05$). The crown length of *Q. serrata* was significantly higher when grown with *E. decipiens* compared to the monoculture ($P = 0.008$) and the *Q. serrata–C. henryi* combination ($P = 0.020$). In addition, the crown length of *Q. serrata* was enhanced in the four-species combination compared to the *Q. serrata* monoculture ($P = 0.028$) and combination with *C. henryi* ($P = 0.042$). The length of the longest branch of *S. superba* was significantly enhanced when grown in combination with *C. henryi* compared to the monocultures, the combinations *S. superba–E. decipiens* and *S. superba–Q. serrata*, and the four-species combination (all $P < 0.05$).

Branch demography

Species richness had no effect on the number of branches (developed at the end of the experiment) but influenced branch turnover ($P = 0.043$) and pruning ($P < 0.001$; Fig. 3). Branch turnover was significantly enhanced in the four-species combination compared to the two-species combination ($P = 0.047$). Pruning was higher in the four-species combinations than in the two-species combinations and monocultures ($P < 0.001$). Species composition significantly affected the number of branches, branch turnover and pruning. Species identity significantly affected branch demography (all variables; Table 2).

Discussion

Effects of species richness

Our study analysed, for the first time, species richness effects on the branch demography of tree saplings. The increase in pruning and branch turnover with higher species number proved the high dynamics in the four-species combinations. Sapling individuals may adapt their crown architecture to changes in their local neighbourhood by modifying their branching arrangement (Sumida et al. 2002). These changes may be caused by the species-specific crown architecture of neighbouring saplings and differences in leaf occurence. We interpret the observed highly dynamic branch demography as an effect of proceeding niche differentiation with regard to light harvesting in this relatively complex neighbourhood of the four-species combination.

Contrary to our expectations, we found no significant effect of species richness on the other growth and crown architectural parameters. This finding may be attributable to two factors. First, it is highly likely that diversity effects

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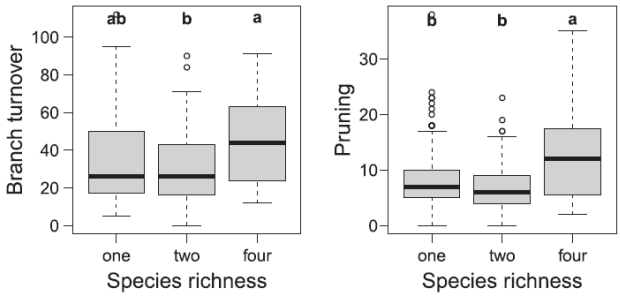

Fig. 3. Boxplots of branch turnover and pruning for species richness levels. Branch turnover is the sum of all positive and negative changes in branch number, whereas pruning is the sum of branch losses over the duration of the experiment. Significances of *post-hoc* Tukey tests of species richness tested by Model 1 are indicated by different letters ($P < 0.05$).

may evolve at a later stage of sapling development. Lang et al. (2010) analysed older tree individuals (20–100 yr) of an overlapping species pool (*S. superba*, *Castanopsis eyrei* Champ. ex Benth., *Q. serrata*, *C. henryi*) in the same study region. These authors found that crown area was affected by functional diversity. They concluded that this was due to niche separation in terms of height stratification, timing of leaf occurrence and crown density (Lang et al. 2010). Second, species richness effects on tree growth responses (e.g. attributable to niche complementarity) might only become apparent at higher levels of diversity (Papaik & Canham 2006). The occupied niche space should increase with higher species number and thereby make niche complementarity more likely to occur.

Effects of species composition

The effects of species composition on growth, biomass allocation, crown architecture and branch demographic variables indicated that the species identity of neighbouring saplings is an important determinant of sapling growth (H2) in our experiment. This finding is in accordance with studies that demonstrate the importance of neighbour tree identity for growth (e.g. Massey et al. 2006; von Oheimb et al. 2011) and crown formation (Frech et al. 2003; Massey et al. 2006; Lintunen & Kaitaniemi 2010) of individual trees.

We hypothesize that several mechanisms – depending on the species involved – determine effects caused by species composition. These are evidenced by differences in the growth performance of less productive species (here: *C. henryi*, *Q. serrata*; deciduous) in the monocultures compared to combinations containing both highly productive (here: *E. decipiens*, *S. superba*; evergreen) and less productive species.

When growing together with *E. decipiens*, the two species *Q. serrata* and *C. henryi* grew taller and produced more biomass than when growing in monoculture or with other species. These results indicate that intra-specific competition of *C. henryi* and *Q. serrata* individuals was higher than the species inter-specific competition with *E. decipiens*. Massey et al. (2006) also demonstrated that height growth of saplings may increase in heterospecific plots. However, due to a higher branching of the saplings within homospecific plots, the authors did not detect any effect of species composition on above-ground biomass. In our study, the reduced competition experienced by *C. henryi* and *Q. serrata* was caused to a greater extent by the species identity of the competitor, i.e. by *E. decipiens*, than by the fact that it was growing with any heterospecific neighbour. Based on the observed high productivity of *E. decipiens* in the low-density treatment, we would have expected a reduced performance of less competitive species in combinations with *E. decipiens*. In addition, the biomass of *E. decipiens* individuals was not affected by species composition. Thus, the increased growth of *C. henryi* and *Q. serrata* in combination with *E. decipiens* indicate the existence of complementary or facilitative mechanisms.

Table 2. Crown architecture and branch demography. Values are means for species and density treatments. Different letters show significant differences of *post-hoc* Tukey tests ($P < 0.05$).

Crown characteristic	Species means				Density means		
	Castanea henryi	*Elaeocarpus decipiens*	*Quercus serrata*	*Schima superba*	Low	Middle	Dense
Height of first branch [cm]	8.94	6.17	13.36	13.15	4.52^{a}	9.85^{ab}	10.91^{b}
Crown length [cm]	72.89	106.15	76.02	80.97	94.76	89.78	82.08
Length of first branch [cm]	38.91^{a}	21.64^{b}	24.42^{b}	36.24^{a}	26.05^{ab}	36.16^{b}	24.12^{a}
Length of longest branch [cm]	52.65	62.14	43.85	52.82	65.05^{b}	58.01^{b}	48.13^{a}
Number of branches[1]	6.89^{a}	21.32^{c}	16.54^{b}	9.56^{a}	17.64^{b}	13.64^{ab}	12.82^{a}
Branch turnover[2]	15.48^{ab}	30.72^{c}	22.31^{bc}	14.14^{a}	27.12^{b}	22.85^{b}	19.05^{a}
Pruning[3]	6.23^{a}	6.85^{b}	4.99^{b}	4.16^{b}	6.77	6.01	5.09

[1]All branches exceeding 1 cm in length, counted in June 2010.

[2]Sum of all changes in branch number (positive and negative) from November 2009 to June 2010.

[3]Sum of all negative changes in branch number (November 2009 to June 2010).

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The enhanced crown length of *C. henryi* and *Q. serrata* in combinations with *E. decipiens* points to complementarity of crown architecture. Complementary effects, as well as reduced inter-specific competition for light within the four-species plots compared to high intra-specific competition in monocultures, also resulted in longer crowns in both species. In contrast, *C. henryi* had shorter crowns in combination with *S. superba* than in combination with *E. decipiens*. This indicates – together with the enhanced length of the longest branch of *S. superba* in combination with *C. henryi* – negative competitive effects of *S. superba*. The effects of species composition on crown architectural variables highlight the importance of competition for light as a structuring factor of neighbourhood interactions.

Effects of species identity

Species identity was a strong predictor throughout the whole experiment. We found all the response variables analysed affected by species identity, which confirms our H3. Our findings also confirm the results of other studies that have described species-specific relative growth rates (Dekker et al. 2008; Suter et al. 2010) and crown architecture (Takyu 1998). Branching frequency, foliage distribution and biomass allocation to leaves significantly affect light harvesting (Niinemets 2010). Energy gain by increased light harvesting is likely to be converted to growth, and thus sapling growth and survival was related to architectural traits (Takyu 1998; Sterck et al. 2003; Dekker et al. 2008). In our study, height and diameter growth were also found to be related to the vertical and horizontal crown dimensions.

When ranking the observed species according to their productivity, the two evergreen species performed better than the two deciduous species. In contrast to our results, seedlings (<0.5 yr) of evergreen species in the same study region have been found to accumulate less biomass and show reduced phenotypic plasticity with regard to shade than deciduous species in a greenhouse experiment (Böhnke & Bruelheide unpublished data). However, the saplings in our experiment were older and thus effects of their growth performance during the seedling stage were of minor importance. The advantages of evergreen leaves, i.e. longer photosynthetic season, lower costs of replacing leaf nutrients and tougher laminae to endure frost, drought and herbivory (Givnish 2002), might also have contributed to the better performance of the evergreen species in our experiment.

Our results indicated a close relationship between species identity and branch demography. Species identity effects on branch demography were pronounced, since each of the four species had a different branch development strategy. The number of branches was low for *C. henryi* and *S. superba*. Whereas *S. superba* had the lowest degree of pruning and thus was able to invest more in stem biomass, *C. henryi* displayed high branch mortality, combined with long branches and smaller height increments. In contrast, *Q. serrata* had an intermediate number of branches and degree of pruning. High turnover rates and branch numbers of *E. decipiens* combined with large height and diameter growth suggest that this species may be able to adapt quickly to changes in the local light environment and thus optimize its foraging for light by means of a highly flexible biomass allocation to branches. The differences between species in branch demography may be seen as niche separation with regard to light harvesting. Furthermore, different branch demography results in distinct crown architecture of saplings which has important effects on ecosystem functions such as the reduction of erosive power of rain throughfall (Geißler et al. 2012).

Effects of density

We found a negative effect of density on diameter growth rates, but no density effects on height growth, thus partly confirming H4. Our findings are in agreement with competition studies, according to which diameter growth was often found to be influenced by the local neighbourhood (Biging & Dobbertin 1992; Canham et al. 2004; Oheimb et al. 2011). The significant reduction of biomass in all constituents of saplings of the high-density plots indicated that competition increased with increasing stand density.

In addition, density significantly affected crown architecture. A positive effect of reduced stand density on crown area was found for mature trees by Yu et al. (2003) and Hein et al. (2008). However, while the number and length of branches of loblolly pine increased with decreased density (Yu et al. 2003), this was not the case in Douglas-fir (Hein et al. 2008). Thus, effects of density on crown architecture might be species-specific and generally depend on distances to neighbours that a tree individual may encounter in the respective stand.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. An alternative analysis of our results.

Appendix S2. Test of phylogenetic signal in the traits.

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CHAPTER 3

Diversity–productivity relationships in sapling communities of subtropical forest species in different light conditions are driven by the presence of particular species

Martin Baruffol, Pascal A. Niklaus, Bernhard Schmid

Diversity–productivity relationships in sapling communities of subtropical forest species in different light conditions are driven by the presence of particular species

Abstract

The development of tree sapling communities depends of biotic and abiotic variables; as with grassland communities a positive species richness–productivity relationship can be expected. Because the variation of environmental conditions affects the performance of individuals in a species-specific way, it is expected that resource limitations (e.g poor light) also affect the performance of the community and the species richness–productivity relationship. We planted 4224 saplings of twelve subtropical tree species in communities of one, two or four species in light and shade. The saplings were harvested after fourteen or seventeen months of growth and their biomass was assessed as a function of species richness, the presence of particular species in the community, light condition and density of survivors. Species richness did not influence individual sapling biomass. However, we found a positive effect of species richness, number of individuals surviving at the end of the experiment and the interaction between these two on community biomass. The positive effect of species richness on community biomass was driven by the presence of particularly productive species and the increased chance of finding these in more diverse communities. Although the species richness effect was consistent across the two light treatments, the strength of the relationship was dependent of species-specific survival and growth.

Introduction

Biodiversity–ecosystem functioning (BEF) research has been developing for nearly twenty years. Until recently the majority of projects focused on temperate grasslands and laboratory environments (Balvanera *et al*. 2006, Peh & Lewis 2012); gradually forest experiments are being added to BEF research (Scherer-Lorenzen *et al*. 2007, Nadrowski *et al*. 2011, http://www.treedivnet.ugent.be/index.html). It is widely recognized that diversity has a positive effect on productivity in herbaceous ecosystems (Hooper *et al.* 2005, Balvanera *et al.* 2006). These effects can be explained in terms of complementarity and selection effects (Hector 1998, Hooper *et al.* 2005). Complementarity effects occur through niche differentiation and reduced interspecific competition or pathogen loads, whereas selection effects can occur because diverse communities are more likely to contain particularly productive species (Loreau 1998, Loreau 2000, Loreau & Hector 2001). Complementarity and selection effects are not mutually exclusive but can act simultaneously (Hooper *et al.* 2005).

Conclusive results on diversity effects in mature forest are unraveled to date due to forest long time taken for forest to establish. However, preliminary results on initial relationships between plant richness and growth are already available (Potvin & Gotelli 2008, Potvin & Dutilleul 2009). The early successional stages of establishment and initial competition are important for the development of later forest stages, because seedling survival and growth define the composition of successive forest stages. Biomass productivity is an indicator of forest growth, because biomass is one of its major structural components.

Forest communities occur in different environments and are subject to different resource availabilities. For instance, light availability is recognized as a major growth-limiting factor for plants (Jennings *et al*. 1999, Barbier *et al*. 2008) and its effect can be species-specific (King 1994). Light availability has proven to be an important determinant both for species composition

and aboveground biomass in grasslands (Beackage & Clarke 2003, Hautier *et al*. 2009), for early growth (Pacala *et al.* 1994) and the survival of woody species (Kobe *et al*. 1995, Beackage & Clarke 2003). It is important to note that light differences in nature are generally the result of biotic processes such as gap formation (Beackage & Clarke 2003, Barbier *et al*. 2008) or the canopy height.

The incorporation of resource limitation (e.g. low light) as treatment in BEF experiments is important because environmental conditions where plant communities develop are heterogeneous and differences in resource availability have effects on biotic interactions (Ishii et al. 2013). Competition for light is asymmetrical and different interactions between species are expected in different light conditions (Yachi & Loreau 2007). Determining how species richness would affect ecosystem functions under different light regimes is thus hard to predict. However, given the relevance of light for growth, it can be expected that during initial growth communities will experience different inter-individual relations under light limitations and that community growth might depend on species-specific traits. With the exception of the Sabah biodiversity experiment (Hector *et al*. 2011) all the large BEF forest experiments (i.e. BEF-China, biodiversity plantation of Sardinilla, BIOTREE http://www.treedivnet.ugent.be/experimental.html) have been planted in cleared fields providing high light conditions during critical growth. However, in natural conditions tree seedlings and saplings will usually grow under canopy vegetation like in the Sabah experiment and this may affect initial interactions between planted individuals and tree growth and survival.

In this project, we therefore explored the biodiversity–productivity relationship of sapling stands under two contrasting light conditions. Our aims were to test 1) if the biodiversity–productivity relationship in tree sapling communities is positive as found in grassland experiments and 2) if low light availability modifies the relationship. Our project was carried out as a common garden

experiment in which communities were planted with different species richness levels under direct exposure to the sunlight or under a shady cage.

Methods

Study site

This experiment was part of a larger competition experiment within a BEF project in China ('BEF-China' project, http://www.bef-china.de/index.php/en). The project is located in subtropical south-east China and our competition experiment aimed to assess initial inter- and intra-specific competition of saplings under different treatments.

The experiment was carried out in the lower valley of the Tiquanshui river (体泉水), near Xingangshan, Jiangxi province, China. The experiment was established on a former agricultural field with corners in the north-west at N29 06.325 / E117 55.244, in the south-west at N29 06.293 / E117 55.235, in the north-east at N29 06.295 / E117 55.326 and in the south-east at N29 06.266 / E117 55.329. Prior to the establishment of the experiment the field had been planted with crops such as rice and wheat. In preparation for the experiment the field was ploughed and harrowed. We also dug small drainage ditches (15–30 cm) along the sides of the plots and channels (50 cm) along the sides of each block to reduce flooding risks.

Experimental design

Our experimental design consisted of eleven communities for each of three species pools, each containing four species: a monoculture of each species (four communities), all possible pair-wise combinations of the species in the pool (six communities) and a community of the four species (one community). Communities were planted in plots containing sixteen individuals distributed in a rectangular grid of four rows by four columns. The abundance of individuals was equally distributed among the species (eight individuals of each species in the 2-species communities

and four individuals of each species in the 4-species communities). A shade treatment was crossed with the species richness treatment. A cage covered from the top to the bottom (up to ~10 cm from the ground) with shading net was installed over each of the shade-treated plots. The cages were initially 1.50 m tall; however, as we noticed that some individuals would reach the top of the cage by the end of the experiment, we increased their height to 2 m from the ground.

The communities were designed to maximize between-individual interactions. We used plots of 1 × 1 m with planting distances of 20 cm between the individuals and ten cm between individuals and the plot margin. Each light x treatment combination was replicated on four plots occurring in different blocks. In one block the individuals were planted by alternating the identity of species within each plot to keep a perfect regular distribution (Fig. 1a), in the remaining three blocks the individuals were planted according to two sequential randomizations. Firstly, we randomized the four central individuals keeping equal numbers of individuals per species (one individual per species in the 4-species communities and two individuals per species in the 2-species communities). Secondly, we randomized the distribution of the outer individuals.

Within the four blocks the treatment combinations were randomly distributed and interspersed with further plots belonging to other experiments within the BEF-China project. There were 66 treatment combinations per block (three species pools x eleven species compositions x two light treatments) yielding a total of 264 experimental plots. We planted 4224 seedlings (264 plots × 16 individuals), 1056 in the center and 3168 in the outer rows of the plots. In our analysis we focused on the central individuals (Appendix 1) and considered outer individuals as a buffer zone.

The experiment was planted in the last week of March 2009 and a month later 379 dead individuals were replaced. If individuals of the same species were no longer available, we replaced them with individuals from another species present in the same plot (118 plots) or if this

was not possible, with an individual of a "functionally" similar species (two plots). Specifically, we replaced dead individuals of *Pinus massoniana* with individuals of *Cunninghamia lanceolata* and dead individuals of *Cyclobalanopsis myrsinifolia* with individuals of *Castanopsis sclerophylla.*

Species selection

The species were selected based on the composition of the surrounding natural forests (Bruelheide *et al*. 2011) and availability of saplings in local nurseries. Twelve species, assigned to three species sets (pools) of four species each were selected. Genus names of the species are abbreviated to their first letters; Table 1 shows complete names for references.

Measurements

A first replicate was harvested in July 2010 and the rest of the plots were harvested in September 2010. For this study, we harvested all aboveground biomass material. Biomass was weighed fresh and oven-dried (70 °C for 48 hours). All individuals in two blocks were harvested completely (one block in June 2010, the other block in September 2010). In the other two blocks only the four central individuals were harvested (in September 2010).

Characterization of light availability in control and shaded plots

We measured the photosynthetic active radiation (PAR) 1 m above the ground under the shading net or in direct exposure in all plots one month after the experiment was planted, within one species pool to compare light conditions in shade and control plots. Mean PAR in control was 526 $\mu*mol*m^{-2}*sec^{-1}$ (± 26.2, minimum 231, maximum 895). In contrast, in shade plots radiation was decreased to 25.4 $\mu*mol*m^{-2}*sec^{-1}$ (± 2.47, minimum 8.1, maximum 80.9). To estimate the light intercepted by the shading net we averaged all the values per block per light treatment and calculated the light interception (LI) as (Flénet *et al*. 1996):

$$LI = ((PAR\ direct\ exposure - PAR\ under\ shade\ net)/\ PAR\ direct\ exposure)*100$$

The mean light interception by the cage in shade plots was 95.4%.

To identify if the shading would affect temperature, we selected six monocultures of *S. superba* (three in the light and three in the shade treatment) and compared their temperatures on a sunny summer day (10th September 2010). Mean temperature in control plots was 33.6 °C, in shade plots 33.9 °C, pointing at no considerably temperature difference between the light treatments.

Data analysis

Mortality was assessed with generalized linear mixed-effects models and individual and plot biomass with general linear mixed-effects models with GenStat (version 14.2, Payne *et al*. 2009).

For the mortality analysis, the terms of the fixed-effects model were linear species richness, light treatment and species identities. For the random-effects model we used species composition (33 communities) nested within the three species pools. As an offset we used the log-transformed harvest time (months after planting). We set the distribution as binomial, with a complementary log-log link function (Egli & Schmid 2001). We selected our final model by backward model selection using the AICs and biological insight as guidance.

For the biomass analysis at the individual tree level, we log-transformed the dry weight to improve homoscedasticity. We included harvest time, block, species pool, species identity, light treatment, community density (surviving trees per m²) and linear and categorical species richness as fixed-effects terms. Species composition (33 communities) and plot were used as random-effects terms. We used block as a fixed-effect term to avoid testing harvest time (one degree of freedom) against block (two degrees of freedom). We used backward model selection, to determine the final model.

At the community level we used a similar model, including the log-transformed dry mass of the accumulated biomasses of the central individuals of each plot as dependent variable, species richness, light treatment and community density (surviving trees per m^2) as fixed-effects terms. In addition, we included terms for the presence of each particular species in a plot. During model simplification, we removed the presence of particular species terms sequentially and left only those species with strong effects on the model. In the analysis we used block, species composition nested with the three pools and their interaction with the light treatment as random-effects terms.

Of a total of 264 planted communities, half control and half shade communities. By mistakes during the plantation we lost one of the four replicate plots in three plots. In addition, in four monocultures all the central individuals died. Thus, a total of seven plots were missing in the individual-level analysis. For the community-level analysis eleven additional plots were removed, as they presented missing values for some individuals, leaving a total of 246 plots.

Results

Mortality

We assessed the mortality of the four central saplings to obtain a measure of realized density for the analysis of the biomass variables. In total, 265 individuals of the 1048 focus individuals died during the experiment (Appendix 2). The monthly mortality proportion among individuals was not influenced by species richness, but rather by species identity ($p < 0.001$), the light treatment ($p = 0.02$), and the interaction between species identity and light treatment ($p < 0.001$). The monthly mortality percentages were higher in control plots (predicted mean 0.32 %) than in shaded plots (0.16 %). Across the experiment, *C. myrsinifolia* was the species with highest monthly mortality percentages (3.83 %), followed by *C. henryi* (3.55 %), *C. glauca* (2.90 %) and *P. massoniana* (2.87 %). On the other hand, *S. mukorossi* (0.00 %), *E. decipiens* (0.00 %) and *D.*

hupeana (0.51 %) had no mortality at all or low monthly mortality percentages. The interaction between light treatment and species identity resulted from an alternating pattern with mortality being higher in shade than in light for *C. henryi*, *C. lancolata*, *C. sclerophylla*, *D. hupeana*, *Q. serrata* and *S. superba*, but lower in shade than in light for *C. glauca*, *C. myrsinifolia*, *E. decipiens* and *L. glaber* (Fig. 2; Appendix 3). Mortality shows a marginal decline with species richness (Fig. 3).

Individual plant biomass

Plant biomass at the individual level was assessed on the 771 surviving saplings at harvest. The mean individual dry mass across all species was 81.87 g (± 5.39 g, minimum 0.19 g, maximum 1612 g).

The selected model showed significant effects of block on the log-transformed biomass ($p < 0.001$), derived from the fact that block four (49.54 g, ± 4.63 g) was harvested three months earlier than the other blocks (mean biomasses and standard errors were 81.36 g ± 9.96 g for block one, 82.3 g ± 10.24 g for block two and 112.28 g ± 15.28 g for block three, respectively).

The three species pools showed significant differences in individual biomass ($p < 0.001$, with means and standard errors of 80.91 g ± 5.64 g for species in pool 1, 70.16 g ± 7.67 g for species in pool 2 and 94.07 g ± 13.15 g for species in pool 3). Furthermore, species-specific differences in biomass were significant ($p < 0.001$). The species with lowest mean biomass was *C. glauca* (12.70 g ± 2.29 g), and the species with highest mean biomass was *S. mukorossi* (252.69 g ± 34.25 g, Appendix 4).

The light treatment had a highly significant effect on individual plant biomass ($p < 0.001$); all species producing lower biomass in the shade treatment (mean for all 33.80 g ± 2.61 g) than in light treatment (126.45 g ± 9.59 g; Appendix 4).

Species pool and species within each pool showed significant interactions with light ($p = 0.018$ and $p < 0.001$ respectively, see Fig. 4). Species with strong proportional biomass reduction in shade were *Q. serrata*, *D. hupeana* and *P. massoniana* (biomass in the shade 9 %, 11 % and 15 % of biomass in light for the three species, respectively). In contrast, the species with lowest biomass reduction in shade were *E. decipiens*, *C. sclerophylla* and *C. henryi* (with biomass in shade 65 %, 49 % and 44 % of biomass in light, respectively).

Community-level biomass

The mean community biomass for the plots in the experiment was 998.28 g/m^2 (± 91.8 g/m^2). Mean community biomass of monocultures was 827.76 g/m^2 (± 169.64 g/m^2), with much higher mean values in the light treatment (1359 g/m^2 ± 325.64 g/m^2, maximum 13024 g/m^2 in a monoculture of *S. mukorossi* and minimum 49.2 g/m^2 in a monoculture of *C. glauca*) than in the shade treatment (320.2 g/m^2 ± 50.76 g/m^2, maximum 1736.48 g/m^2 in a *E. decipiens* monoculture and minimum 6.56 g/m^2 in a *C. myrsinifolia* monoculture). The 2-species communities had higher mean biomasses than monocultures throughout the experiment 1080.24 g/m^2 ± 117.88 g/m^2, in the light treatment (1757.36 g/m^2 ± 199.08 g/m^2, maximum 7170.2 g/m^2 in a community with *S. mukorossi* and *C. sclerophylla* and minimum 39.12 g/m^2 in a plot with *P. massoniana* and *C. glauca*) and in the shade treatment (403.08 g/m^2 ± 51.92 g/m^2, maximum 2118.84 g/m^2 in community with *S. superba* and *E. decipiens* and minimum 11.4 g/m^2 in a community of *S. superba* and *Q. serrata*). Similarly, mean community biomass in the 4-species communities was 1172.76 g/m^2 (±247.8 g/m^2), 1624.8 g/m^2 in light treatment (±402.04 g/m^2, maximum 4619.64 g/m^2, in pool 2 and minimum 178.08 g/m^2 in pool 1) in contrast to 630.28 g/m^2 for communities grown in shade treatment (±135 g/m^2, maximum 1339.32 g/m^2 in pool 3 and minimum 70.28 g/m^2 in pool 2; Appendix 5 shows mean values per community).

In accordance with these mean values, the statistical analysis on the log-transformed biomass revealed an overall positive effect of species richness ($p < 0.001$; Fig 5a). However, if the presence of particular species was fitted in the analysis, it fully explained the positive species richness effect. The three dominant species (i.e. species with largest biomass in each species pool) were responsible for the species richness effects, i.e. in pool 1 *E. decipiens* ($p = 0.002$), in pool 2 *S. mukorossi* ($p < 0.001$) and in pool 3 *D. hupeana* ($p = 0.005$). These three species were, thus, kept in the final model.

The shade treatment had a significant ($p < 0.001$) negative effect on biomass and strongly limited sapling biomass (Fig. 5 a, and b).

There was a positive effect of realized community density (number of survivors out of the sixteen individuals) on biomass, which could be attributed to a greater number of individuals adding to the total biomass, indicating that survivors could not yet compensate for the losses by increased growth with more resources available according to the law of constant final yield (Begon *et al*. 2005). The interaction between species richness and density was significant ($p = 0.034$), density having a more positive effect on biomass in light than in shade (Fig. 5b).

Interactions between light treatment and the presence of the dominant species were also significant in two cases: plots with *D. hupeana* in the shade had significantly less biomass than plots with *D. hupeana* in the light ($p < 0.001$). On the other hand, the effect of the shade treatment was weaker ($p = 0.01$) if the plots had *E. decipiens* present than otherwise. These contrasting effects are explained because of the particular effects of the treatment on the two dominant species. *D. hupeana* is one of the species most affected by the shade (much higher mortality and much lower biomass in the shade than in the light). *E. decipiens* in turn, had higher mortality in the light and its biomass was less affected than that of other species.

Discussion

Our results show a positive effect of species richness on community biomass. This positive effect of diversity on community biomass has been widely shown in grassland biodiversity experiments (Tilman *et al*. 1996, Hector *et al*. 1999, Tilman *et al*. 2001, Balvanera *et al*. 2006) and has been explained in terms of both complementarity and selection effects (Tilman *et al*. 2001). Although the species richness–productivity relationship has not been studied as extensively in forest as in grasslands, there is also some evidence for a positive relationship in temperate and boreal forests from observational studies (Paquette & Messier 2011, Gamfeldt *et al*. 2013, Baruffol *et al*. 2013).

The positive species richness–community biomass relation is not due increased individual biomass, as individual biomass was not affected by species richness, but rather by species identity and the light treatment. Individual growth has been found to be the main reason for the positive effect of species richness on sum of basal area, in the Sardinilla forest biodiversity experiment after five years of growth (Potvin & Gotelli 2008). Individual plant growth was explained in terms of lower heterospecific competition in mixtures compared with higher intraspecific competition in monocultures (Potvin & Dutilleul 2009, Potvin *et al*. 2011). In our study, there is evidence that the positive effect on community biomass was driven by the dominance of particular species across the communities, as one high-biomass species was present in each of the three species pools. The presence of a particularly productive species within a community increased the mean biomass of that particular community, and the chance to find individuals of this particular species increases with community species richness level. The high biomass values of these species in monocultures are cancelled out when all monocultures are considered together. Although we did not test statistically for complementary or selection

effects at this stage, we can infer predominance of selection effects over complementarity effects as a determinant for the positive effect on community biomass.

Despite the difficulties to identify single individuals in grasslands, some experiments have found constant or decreasing individual biomass as species richness increases (Van Ruijven & Berendse 2003, Mwangi *et al*. 2007). Marquard *et al*. (2009) found experimentally that positive biodiversity effects on community biomass were due to increased density of individuals, rather than increased individual sizes in more diverse grassland plots. Moreover, they found that density differences did not influence competition strongly enough to reduce individual biomass growth significantly. We found that mortality in the community was slightly reduced by species richness and that the number of surviving individuals at harvest had a positive effect on community biomass. Similar results were found also in secondary subtropical forests, in which diversity promoted productivity directly and indirectly via promoting more stem density (Baruffol *et al.* 2013).

Interestingly, there was a positive interaction between species richness and density, biodiversity effects on biomass being stronger in plots with high density than in plots with lower density (see Fig. 5c). This positive richness x density interaction suggests, first, a higher chance of finding surviving individuals of more productive species as community species richness increases and, second, less competition in more species-rich communities. Our results contrast with the ones of He *et al.* (2005), in which density was deliberately manipulated as a treatment in addition to the factorially crossed species richness in a grassland experiment. He *at al*. (2005) found a weaker richness–productivity relationship when higher densities of seedlings were planted. This particular trend was explained as denser communities reduced their evenness, evenness having been found to have positive effects on productivity (Chapin *et al*. 2000, Schmid *et al*. 2002). We

were limited in our highest species richness level to one individual per species and higher densities in more diverse plots would thus also imply a larger evenness.

Neighborhood competition (number, size and distance to neighbors) has been reported as having strong effects on individual tree growth (Stoll *et al*. 1994, von Oheimb *et al*. 2011); and planting density can be considered as a surrogate of neighborhood competition. Lang *et al*. (2012) found, for instance, that planting density had a strong negative effect on individual basal area increment at the same experimental site as used here and with the species of our first species pool in an experiment running simultaneously with ours.

Due to the challenges of tree diversity experiments, there is a lack of studies on the effect of tree diversity under different light regimes on productivity. To our knowledge, Sapijanska *et al*. (2013) is the only study other than ours which compares the effect of diversity under different light regimes on productivity. Light availability has been found to influence biomass and biomass-related traits such as radial growth in tree saplings (Kobe 1999, King *et al*. 2005), biomass (Seiwa 2007), relative height growth rate (Poorter 2001, Seiwa 2007) and sapling survival (Queenborough *et al*. 2007). Mass accumulation and height increased with light availability in five species of temperate forests (with one exception for the mass of one of the species), independently of the species' successional status (Seiwa 2007). Kobe (1999) found that of a set of four neotropical species all presented a positive light–biomass relationship, however, the magnitude of the effect differed from species to species. In concordance with these studies we found a strong effect of light availability, which differed between species. The overall species richness (diversity) effect on biomass was consistent under both the light and shade treatments, as found also on basal area increment in shaded and canopy trees in the Sardinilla experiment in Panama (Sapijanska *et al.* 2013). However, the contrasting species-specific effects of shade on individual growth and mortality in two out of the three dominant species determined differences

for the communities containing those species. Variations in the performance of the community are thus expected as a result of the behavior of particular species with particular shade tolerances.

Conclusions

We found a direct positive effect of species richness on community biomass of up to 3-year old tree saplings under light and shade, the latter simulating understory conditions in a forest with larger canopy trees. The positive biodiversity effects were driven by particular species in each of the three species pools. We found in addition a potential indirect effect of species richness on plot community biomass via reduced mortality. Our results suggest that communities exposed to gaps (simulated by the light treatment) or in the understory (simulated by the shade treatment) would benefit from a diverse species composition as they can accumulate more biomass. Species identity seems to be important and communities may depend on how the most dominant species perform under those particular environmental conditions. There are few studies exploring diversity effects under different environmental conditions. Although light availability affected community biomass and had species-specific effects on mortality and biomass, it did not affect the positive relationship between species richness and biomass in our experimental plots.

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Tables

Table 1: List of species used in the experiment and the species pools to which they belonged. The abundance (total number of individuals) and frequency (number of appearances in 27 plots of 30 x 30 m of these species in a nearby forest (Bruelheide *et al*. 2011) are shown together with their leaf fall pattern (e = evergreen, d = deciduous).

Pool	Species	Abbreviation	Abundance	Frequency	Leaf habit fall
1	*Castanea henryi* Rehder & E.H.Wilson	ch	40	11	d
1	*Elaeocarpus decipiens* Hemsley	ed	10	2	e
1	*Quercus serrata* Thunberg	qs	1353	16	d
1	*Schima superba* Gardn. & Champion	ss	943	27	e
2	*Cunninghamia lanceolata* (Lamb.) Hook.	cl	91	11	e/c
2	*Cyclobalanopsis glauca* (Thunberg) Oersted	cg	217	14	e
2	*Dalbergia hupeana* Hance	dh	55	11	d
2	*Pinus massoniana* Lamb.	pm	436	21	e/c
3	*Castanopsis sclerophylla* Schottky	cs	76	4	e
3	*Cyclobalanopsis myrsinaefolia* Oersted	cm	108	8	e
3	*Sapindus mukorossi* Gaertner*	sm	-	-	d
3	*Lithocarpus glaber* (Thunberg) Nakai	lg	690	20	e

S. mukorossi was not found in the forests sampled by Bruelheide *et al*. (2011), it is however a common species in the region.

Figures

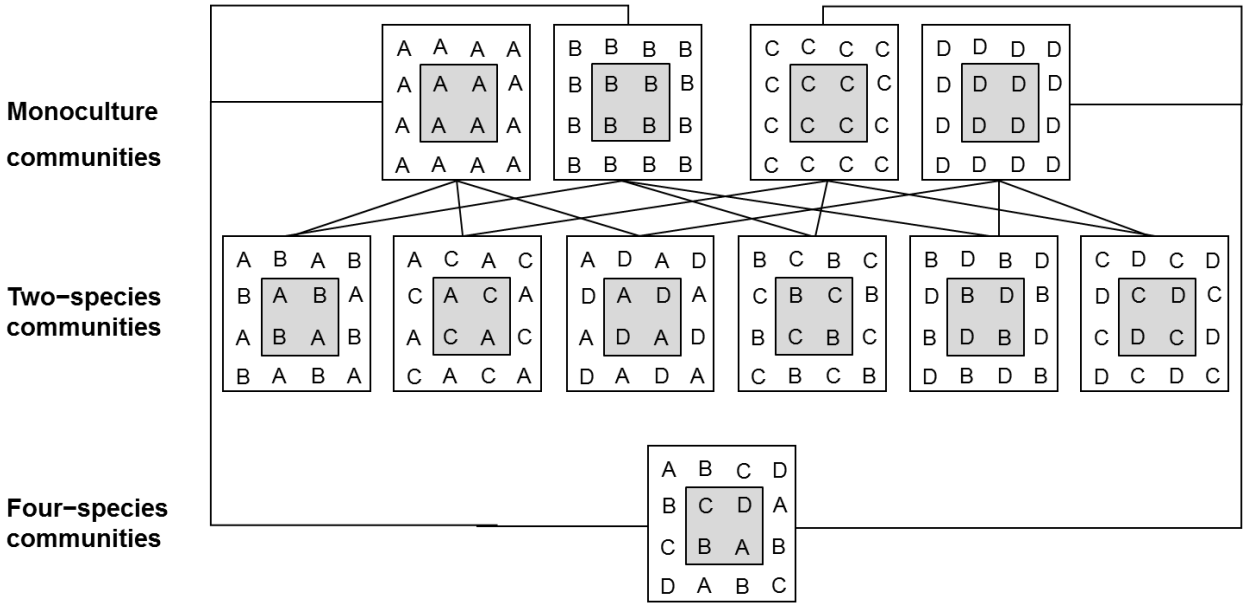

Fig. 1. Eleven different species compositions of one species pool in the experiment used in the present study including all possible monocultures and 2- and 4-species communities in the pool (here species A, B, C, D). The shaded square in the middle of each plot indicates the central four target individuals of each plot.

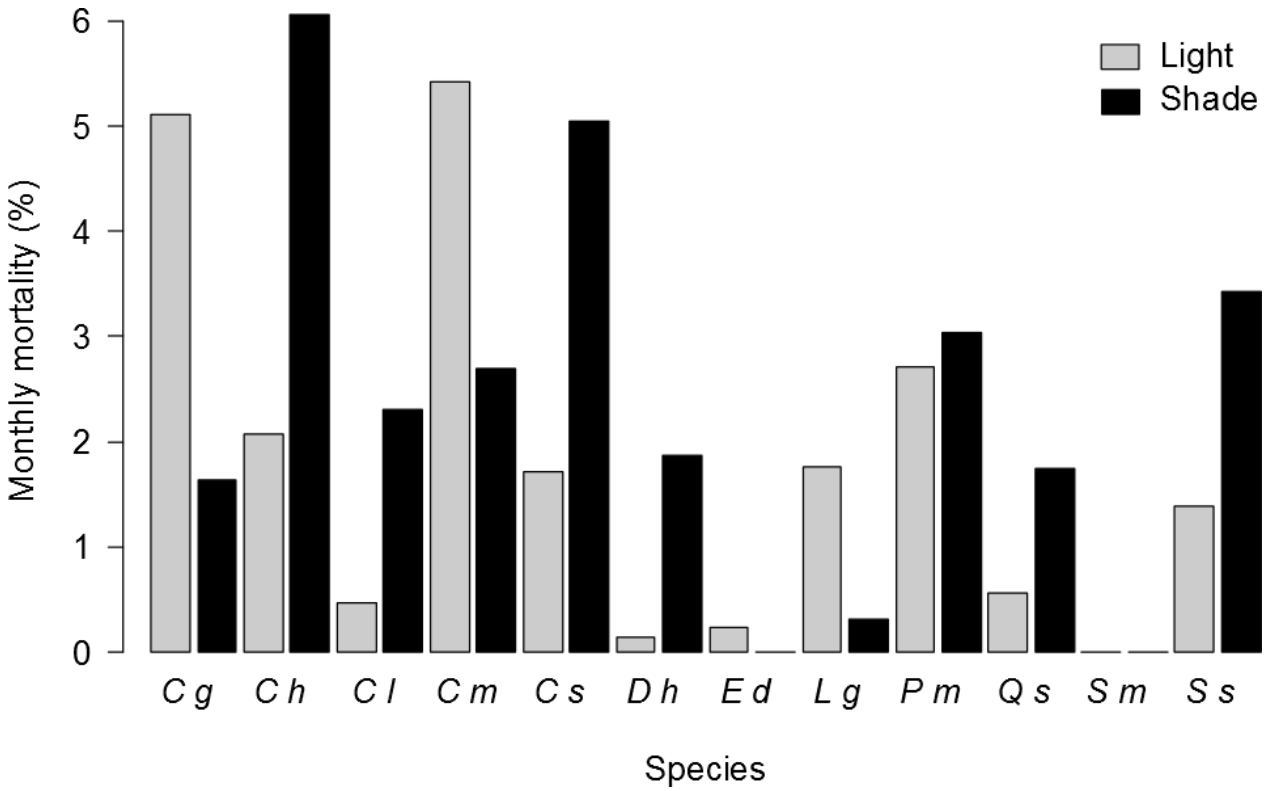

Fig. 2. Monthly percentual mortality for each of the twelve species in control (grey bars) and shaded plots (black bars). Species are identified by the first two letters of their scientific name.

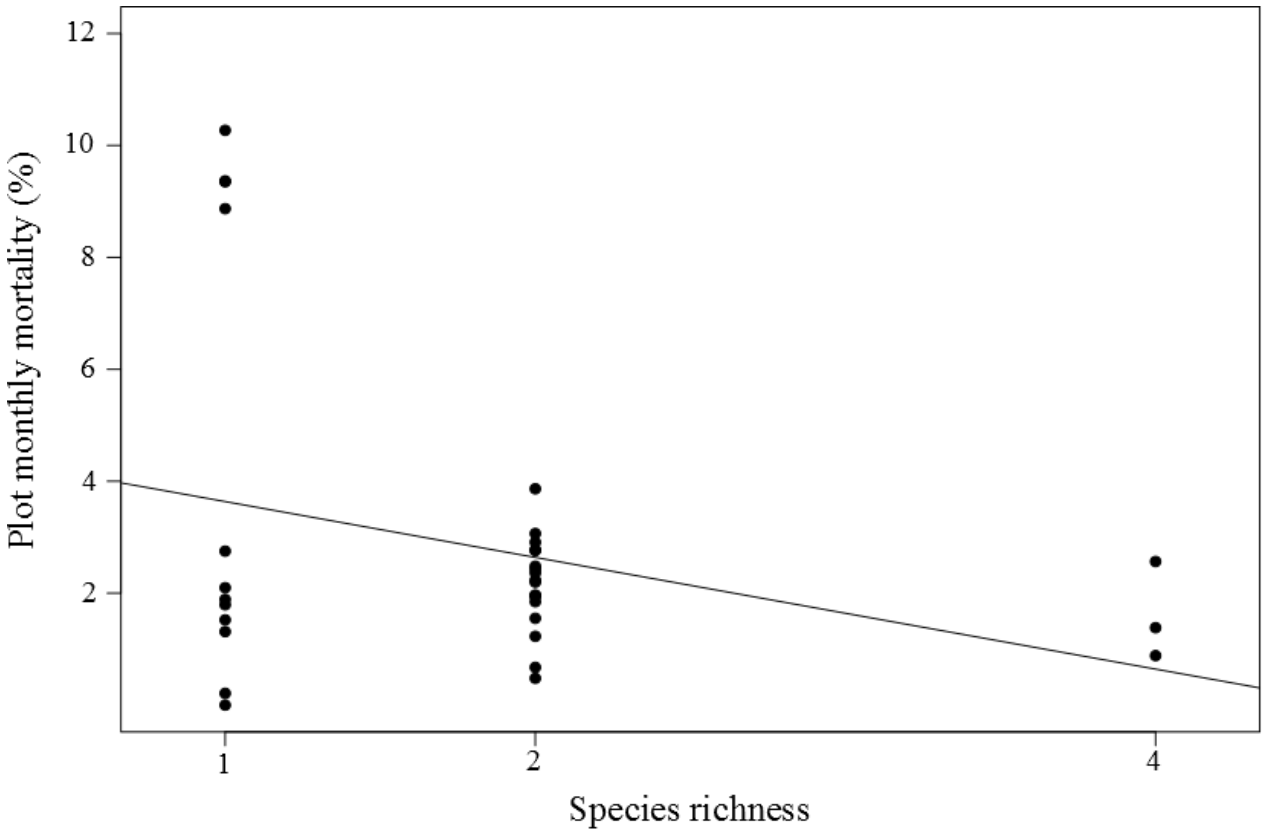

Fig. 3. Monthly percentual mortality ploted against species richness level

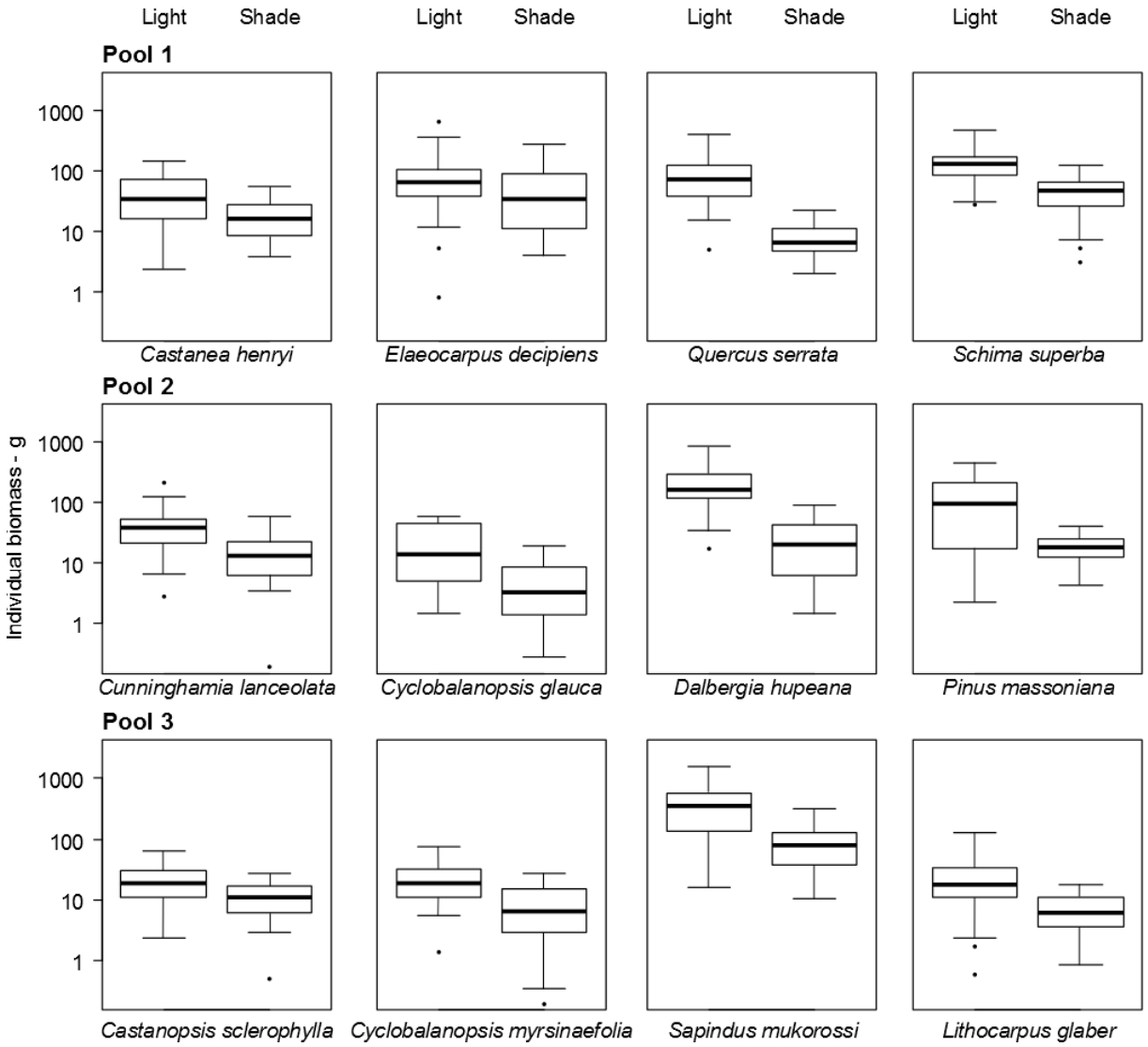

Fig. 4. Individual biomass of the twelve species in the two light treatments. Horizontal lines show the median biomass; the bottom and top of the box show the 25th and 75th percentiles; the whiskers show either the maximum and minimum values or 1.5 times the interquartile range of the data; and points show outliers (R Core Team, 2012).

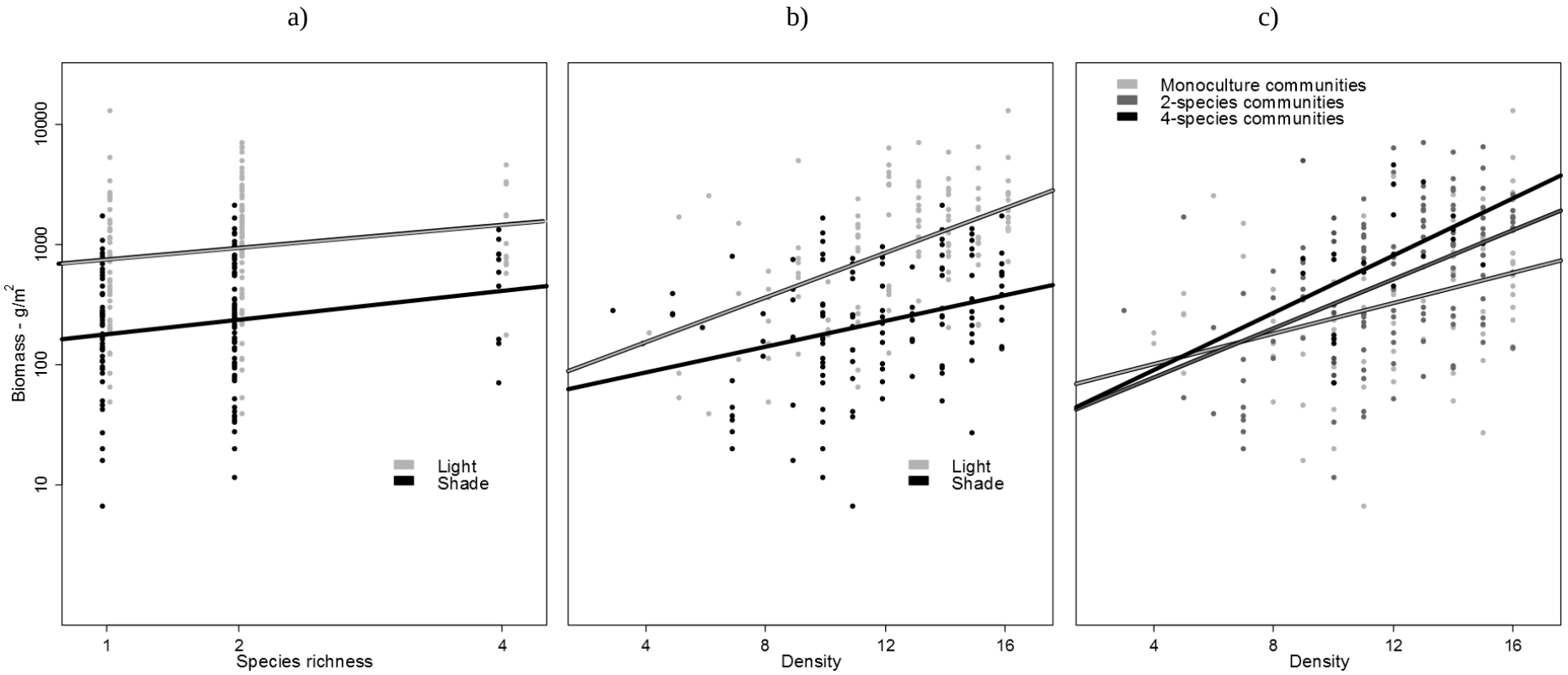

Fig. 5. Effect of species richness (a) and density (b) in light and shade and of density in the three diversity treatments (c) on community biomass. Circles represent the raw data and the lines show fitted lines from the linear model fitted to the data.

Appendix

Appendix 1. Planted individuals per species in the center of the plots by species richness and light treatment.

Species	Number of Planted Individuals					
	Overall	**Control**	**Shade**	**Monoculture**	**Richness 2**	**Richness 4**
Cyclobalanopsis glauca	86	44	42	32	46	8
Castanea henryi	89	43	46	32	49	8
Cunninghamia lanceolata	97	50	47	32	54	11
Cyclobalanopsis myrsinifolia	88	44	44	32	48	8
Casantopsis sclerophylla	88	42	46	32	48	8
Dalbergia hupeana	87	45	42	32	47	8
Elaeocarpus decipiens	88	44	44	32	48	8
Lithocarpus glaber	84	42	42	32	44	8
Pinus massoniana	78	37	41	32	41	5
Quercus serrata	90	44	46	32	50	8
Sapindus mukorossi	84	40	44	28	48	8
Schima superba	89	45	44	32	49	8
Total	1.048	520	528	380	572	96

Appendix 2. Dead individuals per species in the center of the plots by species richness and light treatment.

Species	Number of Dead Individuals					
	Overall	**Control**	**Shade**	**Monoculture**	**Richness 2**	**Richness 4**
Cyclobalanopsis glauca	33	22	11	11	21	1
Castanea henryi	40	12	28	14	23	3
Cunninghamia lanceolata	18	4	14	6	11	1
Cyclobalanopsis myrsinifolia	40	24	16	14	21	5
Casantopsis sclerophylla	29	7	22	7	19	3
Dalbergia hupeana	13	1	12	5	8	0
Elaeocarpus decipiens	2	2	0	1	1	0
Lithocarpus glaber	14	12	2	6	6	2
Pinus massoniana	32	16	16	17	13	2
Quercus serrata	16	4	12	6	9	1
Sapindus mukorossi	0	0	0	0	0	0
Schima superba	28	10	18	9	17	2
Total	265	114	151	96	149	20

Appendix 3. Predicted mean values of monthly mortality percentages. Effects are calculated considering all the significant variables (treatment and species and their interaction).

Species	**Mean Value of Monthly Mortality (%)**	
	Control Treatment	**Shade Treatment**
Cyclobalanopsis glauca	5.1	1.6
Castanea henryi	2.1	6.1
Cunninghamia lanceolata	0.4	2.3
Cyclobalanopsis myrsinifolia	5.4	2.7
Casantopsis sclerophylla	1.1	5.0
Dalbergia hupeana	0.1	1.9
Elaeocarpus decipiens	0.2	0.0
Lithocarpus glaber	1.8	0.3
Pinus massoniana	2.7	3.0
Quercus serrata	0.6	1.7
Sapindus mukorossi	0.0	0.0
Schima superba	1.4	3.4

Appendix 4:

a) Overall mean individual biomass values averaged across species richness and light treatments.

Species	Mean of Biomass (g)	S.E
Cyclobalanopsis glauca	12.70	± 2.29
Castanea henryi	39.35	± 5.59
Cunninghamia lanceolata	32.54	± 3.63
Cyclobalanopsis myrsinifolia	15.56	± 2.39
Casantopsis sclerophylla	19.64	± 2.15
Dalbergia hupeana	147.76	± 20.38
Elaeocarpus decipiens	111.59	± 12.43
Lithocarpus glaber	15.87	± 15.87
Pinus massoniana	72.06	± 72.06
Quercus serrata	54.65	± 8.69
Sapindus mukorossi	262.69	± 34.25
Schima superba	101.52	± 10.88

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b) Mean individual biomass values per species and species richness and light treatments.

Species	Mean Biomass (g)								
	Overall	Control				Shade			
		Rich. 1	Rich. 2	Rich.4	Mean	Rich. 1	Rich. 2	Rich.4	Mean
Cyclobalanopsis glauca	12.70	20.69	26.79	23.61	23.26	5.55	6.88	2.90	5.90
Castanea henryi	39.35	28.51	64.45	44.59	48.62	24.37	20.89	8.19	21.40
Cunninghamia lanceolata	32.55	40.69	51.25	24.97	44.46	22.40	12.42	11.75	15.79
Cyclobalanopsis myrsinifolia	15.56	22.66	26.68	31.36	25.15	11.60	8.95	3.15	9.39
Casantopsis sclerophylla	19.64	18.98	32.29	14.32	24.53	11.85	13.28	2.80	12.20
Dalbergia hupeana	147.76	135.97	256.09	456.85	230.66	28.53	22.05	35.10	26.16
Elaeocarpus decipiens	111.59	104.09	166.11	78.96	135.66	52.12	100.99	160.32	88.61
Lithocarpus glaber	15.87	23.24	31.09	19.68	27.47	9.11	6.60	4.72	7.46
Pinus massoniana	72.06	212.10	99.26	139.03	129.91	22.63	16.66	16.22	19.24
Quercus serrate	54.65	111.90	91.01	27.45	94.08	9.95	7.37	7.92	8.27
Sapindus mukorossi	252.70	399.98	457.74	363.03	430.94	45.84	99.96	214.13	90.66
Schima superba	101.52	125.62	151.24	138.93	140.67	56.29	45.13	39.96	48.83
Mean	81.87	102.10	143.53	121.86	126.45	26.29	35.26	55.42	33.80

c) Minimum individual biomass values per species and species richness and light treatments.

Species	Minimum Biomass (g)

	Overall	Control				Shade			
		Rich. 1	Rich. 2	Rich.4	Min.	Rich. 1	Rich. 2	Rich.4	Min.
Cyclobalanopsis glauca	0.28	2.52	1.45	3.51	1.45	0.56	0.28	0.96	0.28
Castanea henryi	2.40	4.97	9.09	2.40	2.40	10.15	3.94	8.19	3.94
Cunninghamia lanceolata	0.19	19.80	.83	2.84	2.84	4.81	3.59	0.19	0.19
Cyclobalanopsis myrsinifolia	0.19	5.45	.35	31.36	1.35	0.19	0.33	1.66	0.19
Casantopsis sclerophylla	0.48	3.74	2.25	4.43	2.25	3.27	0.48	2.80	0.48
Dalbergia hupeana	1.45	46.27	17.80	124.05	17.80	3.05	1.45	12.89	1.45
Elaeocarpus decipiens	1.94	1.94	10.16	21.12	1.94	8.20	18.93	73.35	8.20
Lithocarpus glaber	0.56	1.66	0.56	4.04	0.56	0.82	0.93	4.17	0.82
Pinus massoniana	2.34	45.83	2.34	9.40	2.34	5.76	4.43	16.22	4.43
Quercus serrate	2.08	5.09	15.73	19.68	5.09	2.08	2.29	5.61	2.08
Sapindus mukorossi	10.31	15.70	121.37	109.61	15.70	10.31	32.20	142.1	10.31
Schima superba	3.03	27.76	31.12	116.86	27.76	18.37	3.03	22.91	3.03
Mean	0.19	1.66	0.56	2.40	0.56	0.19	0.28	0.19	0.19

d) Quantifying the biodiversity value of tropical primary, secondary, and plantation forestsMaximum individual biomass values per species and species richness and light treatments.

Species	Maximum Biomass (g)								
	Overall	Control				Shade			
		Rich. 1	Rich. 2	Rich.4	Max.	Rich. 1	Rich. 2	Rich.4	Max.
Cyclobalanopsis glauca	61.13	57.35	61.13	52.70	61.13	13.99	19.58	4.26	19.58
Castanea henryi	144.04	130.45	144.04	83.87	144.04	53.43	55.07	8.19	55.07
Cunninghamia lanceolata	217.14	57.36	217.14	54.16	217.14	61.18	29.14	23.19	61.18
Cyclobalanopsis myrsinifolia	76.33	63.04	76.33	31.36	76.33	25.29	27.08	4.63	27.08
Casantopsis sclerophylla	65.25	65.25	63.22	27.65	65.25	24.33	27.23	2.80	27.23
Dalbergia hupeana	846.89	297.69	705.56	846.89	846.89	55.44	78.91	91.99	91.99
Elaeocarpus decipiens	760.54	235.47	760.54	216.39	760.54	261.15	355.19	243.17	355.19
Lithocarpus glaber	128.79	54.83	128.79	37.07	128.79	16.30	17.77	5.42	17.77
Pinus massoniana	444.30	358.00	444.30	268.66	444.30	37.57	40.88	16.22	40.88
Quercus serrate	394.30	276.01	394.30	32.66	394.30	22.96	15.46	12.24	22.96
Sapindus mukorossi	1612.46	1612.46	1429.67	832.09	1612.46	121.03	180.64	324.95	324.95
Schima superba	481.35	232.37	481.35	177.16	481.35	107.57	122.90	63.51	122.90
Mean	1612.46	1612.46	1429.67	846.89	1612.46	261.15	355.19	324.95	355.19

Appendix 5. Mean community biomass (g/m^2) for each species composition in the two light treatments. For species abbreviations see Table 1.

Species Pool	Diversity	Community composition	Mean community biomass (g/m^2)		
			Control	Shade	Overall
1	1 species	ss	1633.04	562.92	1097.96
		qs	1678.48	109.48	893.96
		ch	342.16	146.24	244.2
		ed	1561.36	833.92	1197.64
		Mean	*1303.76*	*413.12*	*858.44*
	2 species	ss-qs	1402.08	361	881.56
		ss-ch	1618.68	157.28	888
		ss-ed	1477.36	977.08	1227.24
		ch-qs	954.08	148.56	551.32
		ed-ch	1395.8	746.12	1070.96
		ed-qs	2879.56	885.28	1882.4
		Mean	*1621.28*	*545.88*	*1083.56*
	4 species	ss-ed-ch-qs	948.72	800.6	874.64
2	1 species	cl	685.64	246.44	466.04
		cg	206.84	61.04	133.96
		dh	2175.52	313.84	1244.68
		pm	1060.52	226.32	643.4
		Mean	*1032.12*	*211.88*	*622*
	2 species	cl-cg	677.76	97.16	387.44
		cl-dh	2264.64	182.44	1223.56
		cl-pm	648.44	175.8	412.12
		dh-cg	2278.92	149.32	1214.12
		pm-cg	268.2	88	178.08
		dh-pm	2632.8	169.76	1401.28
		Mean	*1461.8*	*143.72*	*802.76*
	4 species	cl-dh-pm-cg	2604.12	127.28	1365.72
3	1 species	cm	241.68	104.4	173.04
		cs	284.72	118.52	201.6
		lg	228.28	145.72	187
		sm	6399.72	733.44	3566.56
		Mean	*1788.6*	*275.52*	*1032.08*
	2 species	cm-cs	350.92	152.76	251.84
		cm-lg	104.88	142.68	123.76
		sm-cm	3743.76	800.72	2272.24
		lg-cs	545	157.36	351.2
		sm-cs	4716.48	826	2771.24
		sm-lg	2806.72	787.08	1796.88
		Mean	*2044.64*	*477.76*	*1261.2*
	4 species	sm-cm-lg-cs	1599.8	879.76	1239.76

CHAPTER 4

The role of functional distance in diversity−productivity relationships

Martin Baruffol, Pascal A. Niklaus, Bernhard Schmid

The role of functional distance in diversity−productivity relationships

Abstract

The positive effect of diversity on primary productivity in plant communities is explained through two mechanisms: complementarity and selection effects. It is however not yet clear how particular species or species-specific combinations in mixtures determine these effects. The traits of each species determine its growth and the combination of traits within a mixed community determine if the relations of the community are driven mainly by competitive or complementarity effects. We tested if functional distance between species in mixtures is responsible for the diversity effect and how it relates to selection and complementarity effects. We used a mechanistic diallel analysis to assess the aboveground productivity, the net effect, selection effect and complementarity effect of 2-species mixtures, as a function of a light treatment, the individual species belonging to the mixtures, the combination of the species in the mixtures and the functional distance between the two species. Mixture communities growing in direct light were more productive and showed stronger interactions between individuals, as was evident from the net and selection effects. Functional distance between the two species and the presence of a dominant species in the mixture increased significantly the biomass, the net and the selection effect on initial stages of 2-species mixtures. The mechanistic diallel analysis allowed to partition the effect of the particular species within the communities to explain better individual species effects under a setting with limited number of mixtures. In addition, the specific combining ability and the functional distance of the two species mixture presented a strong correlation. Community biomass was on average higher in the 2-species mixtures than in the monocultures, in the light and shade.

Introduction

The critical decline of global species diversity over the last century motivated the development of biodiversity−ecosystem functioning (BEF) research, which since the last ~20 years aims to understand the role diversity plays in vital ecosystem processes (Loreau *et al.* 2001, Hooper et al. 2005). It is motivated by the assumption that a large set of species may be required to maintain stability in ecosystem processes under environmental variations (Isbell *et al*. 2011). In fact, experimental and theoretical evidence supports the positive effects of diversity on several ecosystem processes (Hooper *et al*. 2005, Balvanera *et al* 2006, Cardinale *et al*. 2013).

Diversity and more specifically species richness is an important structural property of ecosystems because species possess particular traits, which may increase complementarity between them. Each individual and each species has a set of traits, which determine its competitive ability over a set of dynamic environmental variables, allowing the coexistence of various species simultaneously through differential competitive advantages of some species over others for different environmental conditions (Aarssen, 1983, Case & Taper, 2000). On the other hand, different ecosystem processes require different sets of traits, at different times, in different places and under different environmental settings. Considering the dynamism of ecosystems and the range of ecosystem processes, the extinction of any species can imply the decrease of ecosystem functions in at least one such context (Isbell *et al*. 2011).

The most common measurement of diversity used up to today in BEF have been species richness and derived indexes (i.e. Shannon, evenness) because they are easy to obtain. However, other measurements such as phylogenetic or functional diversity can be incorporated in BEF research (Tilman *et al*. 1997, Petchey & Gaston 2006, Flynn *et al*. 2009, Cadotte *et al*. 2012) as they reflect additional aspects of community diversity. For instance, phylogenetic difference reflects the evolutionary differentiation between species (Srivastava *et al*. 2012, Winter *et al*. 2013) and

functional diversity is related to the range of the potential functions of the species (Petchey *et al*. 2009), which can be expressed numerically and thus be used for direct comparisons across communities. Functional diversity allows, in addition to focus on relevant traits according to the ecosystem function or set of ecosystem functions to be analyzed.

Evidence for a positive diversity−productivity relationship comes mainly from grassland experiments (Balvanera *et al*. 2006, Scherer-Lorenzen *et al*. 2007) because grasslands have been the main focus of BEF research given that they are easily manipulated, develop within relatively short time spans and are often used as multi-species agricultural systems. However, forests are one of the major CO_2 sinks worldwide and the major among terrestrial ecosystems, covering about a third of the land surface, being responsible for more than two thirds of the net primary productivity on Earth and containing more than half of all terrestrial plant and animal species (FAO 2010, CBD 2010). Thus, forests deserve as much attention as grasslands. Due to the long life spans of trees, experiments on forests are only now producing first results from their initial stages (Potvin *et al*. 2011). The few results from forests have all been obtained in observational (Erskine *et al*. 2006, Vilà *et al.* 2007, Paquette & Messier 2010) and comparative studies (Baruffol *et al*. 2013). Preliminary observations from experimental studies suggest similar BEF patterns in forests as in grasslands (Paquette & Messier 2010, Nadrowski *et al.* 2010, Baruffol *et al*. 2013), but it is still too early to state definitive conclusions.

As BEF relationships are established for several ecosystem functions, the debate has moved forward towards the mechanisms by which biodiversity enhances these ecosystem functions. Complementarity (CE) and selection effects (SE) are the two main mechanisms which can explain positive feedbacks of diversity on ecosystem functioning (Loreau & Hector 2001, Spehn *et al*. 2005). CE occurs through differences between intraspecific and interspecific competition, by promoting niche complementarity or facilitation between species. SE occurs due to the higher

chance of finding a particular species with high performance in a species-rich rather than a species-poor community. The two mechanisms are not mutually exclusive, but can act simultaneously.

SE occurs typically when one or a set of particular traits benefit one species over the others in the community, granting it with a competition advantage that allows it to dominate in the community (Hector & Loreau 2001). In the case of productivity, it would imply over-performing biomass production of the dominating species. Loreau and Hector (2001) suggested a method to quantify these effects, plus a net effect (NE) which is the sum of them. The method is derived from Price's general theory of selection (Price 1995) originating from the field of evolutionary genetics. SE is consequently calculated by a covariance function, which considers the deviation from the relative expected yield and the monoculture yield; the CE on the other hand is calculated out of the average of these variables. NE, CE and SE can be either positive or negative and display the deviation from the absolute expected values based on the monocultures. As Loreau & Hector (2001) did with Price's general theory of selection, we also borrowed a concept from quantitative genetics and crop breeding to compare the performance of two species in mixture vs monoculture. The concept of general (GCA) and specific combining ability (SCA) defines as GCA the average performance of all hybrid offspring or in our case the mixtures and SCA as the deviance of a specific hybrid or a mixture from the value predicted by the GCA of the parents or monoculture species (Griffing 1956). This method is commonly applied in diallel crossing systems but can also be used to assess performance of communities in which two species are mixed in equivalent quantities. In this context it is called mechanistic diallel analysis (Schmid *et al*. 2002). For this particular study, we analyzed communities composed of two species, out of a BEF experiment in which tree seedlings of three 4-species pools were planted in monocultures and in all possible 2-species mixtures, i.e 3 * 6 = 18. Our aim was to answer the following questions:

What determines the higher productivity in mixtures over monocultures?

What is the role of species and functional distance for the productivity of mixtures?

What determines that a particular mixture of species performs better than other combinations?

Are the roles of species and functional distance constant across different environmental conditions?

Methods

Design

The analysis presented in this chapter is an in-depth insight into the effect of interspecific relations on harvested aboveground biomass of 2-species mixtures in an biodiversity experiment which was conducted in early-stage forest communities under different light conditions.

Eighteen different 2-species mixtures and their corresponding monocultures (12 species) were planted in replicated plots of 1 x 1 m. The combinations were produced by considering all the possible combinations of three 4-species sets: 1) *Castanea henryi*, *Elaeocarpus decipiens*, *Quercus serrata* and *Schima superba*; 2) *Cunninghamia lanceolata*, *Pinus massoniana*, *Sapindus mukorossi* and *Cyclobalanopsis glauca*; 3) *Lithocarpus glaber*, *Cyclobalanopsis myrsinaefolia*, *Castansopsis sclerophylla* and *Dalbergia hupeana*. Species were selected based on the composition (frequency and abundance) of surrounding forests and the availability of seedlings within the nurseries established for a BEF experiment (BEF-China, Bruelheide *et al*. 2013).

We used two treatments to estimate differences of mixture effects under two different environmental conditions: direct light, as it would be expected in a secondary succession after a clear-cut, and shade, applied with a shading cloth to imitate understory conditions in a mature forest. Each monoculture or mixture was planted under the two different light conditions and

replicated in four blocks. Plots were randomly located within the blocks, which contained 24 monocultures and 36 2-species mixtures each. Each plot contained sixteen individuals with interplant distances of 20 cm to guarantee early stage interactions. In one block, species were planted in regularly alternate positions like on a chessboard, while in the three other additional blocks the individual three positions were defined randomly, controlling for equal abundance of each species in the central 2 x 2 positions of the plot.

The experimented was planted in March of 2009 with a replanting of dead individuals a month afterwards. The aboveground fraction of the four central individuals was harvested, dried and weighed. A first block was harvested in June 2010 and the rest were harvested in September 2010. Further details on the design and planting of the experiment are reported in chapter 3.

Data analysis

As we knew already that on average mixtures produced more biomass than average monocultures (Chapter 3) we were now interested in determining which mechanisms are potentially explaining these results. We therefore assessed plot biomass, NE, CE, SE (Hector & Loreau 2001), GCA and SCA (Griffing 1956). In addition, we tested if these measures were related to the functional distance between the species (see below). In order to meet the assumptions of the statistical analysis models, biomass was logged and we took the squared root of the absolute values for NE, SE and CE. The original sign (+/-) of the untransformed variable was maintained for the transformed variables. When necessary, we also removed outliers (+/- four standard errors away from the mean).

We used general linear models in Genstat (VSN International, 2011) to analyse variation in the different response variables. We used two types of models. In the first one (model type I) we assessed the response variables as functions of light treatment (L-TR) and community composition as fix terms; in the second model type (model type II) we assessed the response

variables as functions of the light treatment, individual species-presence/absence and community composition as fixed terms. We explored effects of two-way interactions between the light treatment and the community-based fixed terms. Within the individual species- and community-based fix terms we separated their effects according to hierarchally arranged levels of organization. In model type I we accounted for the species pool to which the mixture belonged to (POOL), the functional distance between the two species which formed a community (F-Dis), the presence of the dominant species within the mixture (DOM-MIX) and the mixture of the species composition (MIX) itself. In model type II we added the individual species-based fix terms to the previous model. After testing for the light treatment effect we considered first the species pool to which the species belonged, then, whether the evaluated species was the dominant species within the community (DOM-SP), and finally the presence or absence of the additional species within the pool (SP). In addition to the contrast between communities tested in model I, adapting the mechanistic diallel analysis (McGilchsrist 1965), model II allows also to compare effects of the presence of each particular species in the community. Each term was tested against the corresponding error term as indicated by Schmid, *et al*. (2002). The different fixed terms were tested manually in each model against the correct error term. The light treatment term, the community composition term and the interactions of the particular species with the light treatment were tested against the light treatment x community composition interaction; the individual species terms were tested against the community composition and the interactions between the light treatment x community based- terms were tested against the residuals of the models.

The functional distance between species was calculated out of eight traits: mean individual height, evergreen/deciduous, coniferous/angiosperm, leaf dry mass fraction (LMF), SLA, wood density, leaf dry matter content (LDMC) and mean leaf height (MLH, the mean height where the leaves are located in the individual, estimated from the dry weight of the leaves in 50 cm vertical

layers). Traits were calculated from the mean values of the monocultures in the control plots (direct sunlight). Euclidean distances were used for the continuous variables and simple distances for the categorical ones. Functional distance was calculated as the percentual difference between the functional traits of each pair of species.

As final step of our analysis we related the GCA of each particular species (the average performance of all the 2-species mixtures containing the particular species) to the performance of that species in monoculture. For this model we considered the monoculture biomass, the light treatment, the species pools and all the possible interactions. In addition, we related the SCA (the average performance of species *i* in mixture with species *j*) to the most significant community-based variables. As explanatory terms, we used functional distance, light treatment, species pool and all possible interactions. For these last two models we performed a backward model selection, by removing non significant interactions and selecting the simpler model as long as the values of the Aikaike information criterion (Aikaike 1974) were not larger than two units than the previously accepted model.

Results

Monocultures vs 2-species mixtures

The mean biomass of 2-species mixtures in each of the three species pools was higher than that of monocultures (species pool 1: 2-species mixture 1083.56 g/m^2 vs monocultures 858.44 g/m^2; species pool 2: 2-species mixture 802.76 g/m^2 vs monocultures 622 g/m^2; species pool 3: 2-species mixture 1261.2 g/m^2 vs, monocultures 1032.8 g/m^2). This pattern was present in the light treatment and for the species pools 1 and 3 also in the shade. In contrast with this general pattern, monoculture communities in species pool 2 accumulated on average more biomass than 2-species communities when growing in the shade treatment (Baruffol *et al*. previous chapter).

NE, SE and CE

On average, the SE was significantly positive ($p < 0.01$). Although NE and CE also showed a positive trend, these were not in the tested 2-species mixtures significantly greater than 0. Despite these differences in significances, the positive trend of NE was almost equally produced by CE and SE. We saw, however, that these magnitudes differed according to the light treatment, being higher in the light than in the shade (NE almost 4 times, CE almost 25 times and SE over 1.5 times higher in light than in shade). The SE varied less than the CE, and was higher than the CE in the shade, while the CE was higher than the SE in the light. Results within the species pools were similar. However, there were few cases in which on average the effects were negative, particularly in species pool 2 in the shade treatment. Magnitude and direction of differences across pools reflect the relevance of species identity and of the particular species mixtures, which are summarized in Table 1.

Functional distance between species in mixture

The functional distance between species was calculated based on plant-growth related traits of the monocultures in the experiment. On average the functional distance between the species belonging to each pool was 16.52 %, 35.83 % and 24.85 % (with standard errors of 2.88 %, 9.22 % and 9.26 %) in species pool one, two and three, respectively. The maximum functional distance varied between the species pools, being 26.5 % in pool 1 for the mixture between *S. superba* and *Q. serrata*, 64.9 % pool 2 for the mixture between *C. lanceolata* and *S. mukorossi*, and 53.6 % in pool 3 for the mixture between *D. hupeana* and *L. glaber*. The good spread of functional distance values within the pools reflects the fact that none of the species pools was clustered in the dendrogram based on the similarity matrix (Appendix 1).

Analysis of variation in plot biomass, NE, SE and CE in mixtures

The analysis of model type I revealed significant effects of all main effects on the logged biomass of communities (adjusted r^2 0.727). Plots in the direct light treatment had more biomass than the ones in the shade treatment ($p < 0.001$, biomass in light treatment 1070.52 g/m^2 and range within two standard errors 971.01 to 1180.15 g/m^2, in shade treatment 240.78 g/m^2 and range within two standard errors 209.54 to 276.69 g/m^2, as calculated form the raw data). The different species pools also had different biomasses ($p < 0.05$), giving a first hint on species and community differences. More interesting, functional distance had a positive effect on biomass ($p < 0.001$). In addition, the presence in the mixture of the dominant species in the species pool had also a positive effect on biomass ($p < 0.005$, with an average biomass in mixtures in which the dominant species were present of 1016.8 g/m^2, and a range within two standard errors from 754.76 and 1368.68 g/m^2, and in mixtures without the dominant species an average biomass of 248.64 g/m^2 and a range within two standard errors from 184.64 and 334.82 g/m^2, as calculated from the raw data). Besides the main effects, the interaction between the light treatment and the species pool ($p < 0.05$) and the interaction between the light treatment and the functional distance were also significant ($p < 0.005$), the effect of functional distance in the shade being less positive than in the light treatment (see Table 2, Fig. 1a and 2a).

As with the biomass, when we used model type I to explain the NE (adjusted r^2 0.056) we found significant effects for some of the same fix terms. NE effect was significantly increased by functional distance ($p < 0.05$) and marginally increased by the presence of the dominant species in the mixture ($p = 0.088$). The interaction between the light treatment and the species pool was marginally significant ($p = 0.069$; see Table 2 and Fig. 1b and 2b).

Variation in SE (adjusted r^2 0.374) was also explained by the fix terms included in model type I. It differed between the three species pools ($p < 0.01$) and increased with functional distance ($p <$

0.001). The interactions of the light treatment with species pool ($p < 0.001$) and with functional distance ($p < 0.05$) were also significant (Table 2 and Fig. 1c and 2c).

In contrast to the previous dependent variables, CE was not significantly influenced by any term in the model (see Table 2 and Fig. 1d and 2d).

Species-specific effects on mixtures

For the analysis of model type II in which we included the species-level variables, the data were doubled to allow the inclusion of species-specific composition variables, a method used in diallels analysis (Thompson & Phillips 1982). This analysis allows further partitioning of the community variables, by including effects of particular species. By correcting degrees of freedom the doubling of data does not affect significances.

In the analysis of the logged biomass (adjusted r^2 0.715), all the main fix terms showed significant effects (Table 3). In addition to the differences between the light and shade treatment ($p < 0.001$), we found strong species-level effect of species pool ($p < 0.05$), dominant species ($p < 0.01$) and the remaining individual species ($p < 0.001$) on biomass. After inclusion of the effect of individual species (corresponding to their general combining ability), the remaining effect of mixture composition was still significant ($p < 0.001$). Partitioning this effect of mixture composition still showed the significant effects of functional distance ($p < 0.001$), presence of dominant species in the mixture ($p < 0.01$) and residual mixture composition ($p < 0.001$, table 3).

Besides the above main effects, some of their interactions were also significant (Table 3). Light treatment in interaction with aggregated mixture composition ($p < 0.001$) and with the aggregated community variable ($p < 0.001$) had significant effects on mixture biomass. Moreover, when the variables were disaggregated, the light treatment in interaction with species pool and in interaction with species identity were also significant ($p < 0.05$ in both cases).

Finally, the light treatment interactions with functional distance ($p < 0.05$) and mixture composition were also significant ($p < 0.01$). As in the model type I, the positive effects of functional distance on mixture biomass were stronger in light than in shade treatment.

Model type II had higher explanatory power than model type I for NE and SE. NE (adjusted r^2 0.131) was positively affected at the species-level by the presence of the dominant species in the mixture ($p < 0.01$). The combined mixture composition was also significant ($p < 0.05$), product of the positive effects of functional distance ($p < 0.05$) and marginally the contrast of the dominant species in the mixture ($p = 0.06$), which positively affected NE.

In model type II, the SE (adjusted r^2 0.425) was significantly affected by the aggregated species term ($p < 0.001$) which, when disaggregated, was dominated by the significance of the species pool ($p < 0.01$) and the positive effect of the presence of the dominant species in the mixture ($p < 0.01$). Besides the species-related fixed terms, the aggregated mixture composition term was also significant on SE ($p < 0.001$), dominated mainly by the strong positive influence of functional distance ($p < 0.001$). Besides the main effects, the interaction between the light treatment and the aggregated species term was also significant ($p < 0.001$), which when disaggregated was explained by the interactions between light treatment and species pool and functional distance ($p < 0.05$; see Table 3).

The explanation of variation of CE did not improve much in model type II. However, the mixture ($p < 0.05$) and the interaction between the light treatment and the species pool ($p < 0.05$) had a significant effect on CE (see Table 3).

GCA and SCA in relation to monoculture biomass and functional distance

The 2-species mixtures allowed an easy exploration of the outcome as a product of the effect of the two contributing species. We assessed the GCA of the particular species as a function of the

biomass of the species in monoculture, the species pool and the light treatment and all their potential interactions. After backward selection, the remaining terms in the model were biomass of the species in monoculture, light treatment, species pool and the interaction between biomass species in monoculture and species pool (adjusted r^2 0.945). We found a highly positive relation of GCA with biomass of the species in monoculture ($p < 0.001$), which accounted by itself for 68 % of the variation explained in the model. Moreover, the effect of the light treatment was also highly significant ($p < 0.001$). The species pool and the interaction between light treatment and species biomass in monocultures were left in the model, however, without significant effects as suggested during the backward selection model and the evaluation of the AIC (see Fig. 3a).

Considering the relevance of the functional distance for biomass in mixtures, NE and SE, we explored also the relationship between SCA and functional distance. After the backward selection, the remaining terms in the model were functional distance, species pool, light treatment and the interaction between functional distance and the light treatment (adjusted r^2 0.59). Functional distance had a strong effect on SCA ($p < 0.001$) and accounted for 58.5% of the variation explained by the selected model. In addition to the effect of functional distance, the species pool ($p < 0.05$), and the interaction between functional distance and light treatment ($p < 0.001$) also significantly influenced SCA. The functional distance and the interaction between functional distance and the light treatment combined together, accounted for 35.4 % of the variation explained in the model (Fig. 3b).

Discussion

Our analysis revealed a strong relation between the positive effect of mixing two species of young subtropical trees, the functional distance between two species, as well as the dominant species in each of the species pools on the aboveground biomass, on the net effect (NE) and on the selection effect (SE). This result highlights the relevance of functional diversity for

community productivity and that unequal contributions between species can substantially contribute to this effect.

In our particular case, functional distance had a strong effect on SE, which had a determinant role in NE and mixture biomass. Extreme traits have been reported as favouring selection effects, in which initial trait variation determines interspecific differences in productivity in the community and the dominance of the most productive species in the community (Nijs & Roy 2000, Loreau 2000). In our experiment the mixtures with the most trait-differentiated species experienced a strong dominance of one of the species. Species pool 1, which showed more similarity among its species, had a negative SE in the light and when averaged with the shade treatment. On the other hand, species pools 2 and 3, with a stronger dissimilarity between the dominant and the rest of the species in the pool, had positive selection effects in the light and pool 3 also in the shade treatment.

The individuals of the dominant species in the mixture grew more as the functional differences increased, and as they outperformed the other mixture combinations. However, the effect of functional distance remained after fitting the presence of the dominant species in the community (in the species level analysis), and when communities with the presence of the dominant species were fitted in the model before the functional distance (results not shown). The significance of the functional distance independent on the position in the model indicates that functional distance and species dominance are both important terms, independently of potential contributions between the two variables.

The correlation between GCA and the biomass in monocultures shows the consistency of the average performances of each single species with its performance in monoculture. On the other hand, the functional distance effect on community biomass is also evident through the positive

correlation with SCA; because SCA allows evaluating the differences in performance between the particular combinations of species.

Trait differentiation is also considered as the base for niche differentiation which enhances the performance of the community through complementarity effects (Loreau 2000). However, our model did not explain much of the variation in CE. Overall, all the NE, SE and CE were positive when pooled over all mixtures. The CE varied strongly, with large negative values in two mixtures of pool 3. The values of these two mixtures may explain our inconclusive results concerning CE. In comparison to grassland studies which commonly are analysed after few generations, we only studied a fraction of a generation; our individuals did not reach maturity by the end of the experiment. Thus, the time-span of our study could have been too short to show a significant effect of CE on community biomass. Our study lasted eighteen months (~ 547 days), which we considered enough for initial competitive interactions. Complementarity effects, however, have been found to become stronger over several growth generations (Spehn *et al*. 2005, Cardinale *et al*. 2007), and it is estimated that it takes ~1750 days (equivalent to 2 to 5 ramet generations) until mixtures produce more harvestable biomass than the most productive monocultures in grassland (Cardinale *et al.* 2007).

Considering that the relations on the aboveground section of the community is determined by the competition for light, whereas the relations in the soil are defined by soil nutrients and water, it is possible that different kinds of interactions occur belowground (Newman 1973). Our estimation of functional distance was based on six growth traits, all of them derived from the aboveground compartment of the individual plants, as our response variables were also derived from the same fraction of the plant. Weiner (1986) found on *Ipomoeae tricolor* strong asymmetric shoot competition (light), whereas root competition (soil nutrients) was more symmetric and stronger as it exerted a stronger control on plant size. These results were explained as follows: root

competition began at an earlier stage than competition for light, which only began when individual plants were shading each other. The asymmetric competition for the light explains the positive relationship of functional distance on SE. We were focused on light competition and the aboveground fraction of the community and miss relations which occur underground and can have important effects on the community as a whole. Particularly, the inclusion of belowground growth traits would probably have resulted in significant explanatory power on the CE also.

Light limitation modified the effect of functional distance on biomass and SE. Mixtures and monocultures growing in the light yielded more biomass than mixtures and monocultures growing in the shade. Growth of individuals in shaded communities is strongly limited by light (Rüger *et al.* 2011) and competition seemed to be less important than in communities in direct light.

In addition to partitioning the NE into SE and CE (Hector & Loureau 2001), we used here for the first time the approach of mechanistic diallels (McGilchsrist 1965) to the analysis of biodiversity effects (Schmid *et al*. 2002). Although developed initially for the analysis of offspring, when combining different genetic lines, diallel analysis can be borrowed for the analysis of the performance of species mixtures, having reference values of the performance of communities of the individual species growing in monocultures. The logic was applied twice in our study; on the one hand we used it for the calculation of GCA and SCA. On the other hand, we used it to explore the species-specific effects on mixture performance (model type II). For this mean, we used the biomass of the community in the mixture twice, assuming it as the resulting effect of each one of the two species occurring in the community, by treating one species as target and the other one as accompanying species in one case, and alternating the position of the two in the other case. An alternative to avoid the replication of the response variable would be to have each time two plots for community and consider exclusively one of the species as the target each time.

The logistic and economic costs of establishing BEF experiments prevented us from doing this. To avoid the pseudoreplication when the same value as response variable was used for several species in a community, we corrected for the inflated degrees of freedom as suggested in Thompson & Phillips (1982).

GCA, as the average performance of a particular species in mixtures with all the other potential species, can produce better predictions for expected biomass in mixtures than the values of the monocultures which are used for the calculation of NE. GCA incorporates neighbors with a wider spectrum of functional traits, providing thus, more realistic measure of the species performance particularly when the species interacts differently with conspecific than with heterospecific neighbors. GCA can therefore control the strength of the selection effect whenever monoculture performance is considerably different than the one of the species in mixed communities. In addition, it solves the problem of species with very low performances or not surviving in monocultures, which often affects biodiversity–ecosystem functioning experiments. On the other hand, the correlation with functional distance (which can be considered as a *proxy* of diversity/functional diversity on a two species mixtures) was stronger for SCA than for the NE and SE (Figs 2b, 2c and 3b). SCA is a straightforward measurement, which directly considers the deviation of the performance of a particular mixture from the expected mixture performance based on the GCA. Thereby, SCA reflects the effect of the differences between the functional spectrum of the species which integrate the mixture. Although it is simple to calculate and has a straightforward explanation, SCA has been ignored as a valid measure for biodiversity effects.

Conclusions

The functional distance between the species in 2-species mixtures has a positive effect on the total aboveground biomass, NE and SE. Besides functional distance we found that species which dominate the community have also positive effects on these same variables; however, the effect

of functional distance remains after controlling for the presence of the dominant species in the community. These effects are stronger in direct sunlight than in shaded environments, such as under canopies.

The methods brought by the analysis of mechanistic diallels are suitable for analysis of biodiversity effects in mixtures; diallel analysis offers moreover solutions for the interpretation of species-specific effects in ordinary analysis of community level variables in biodiversity experiments.

The importance of the particular species composition for total biomass is confirmed by the SCA, which correlated even more strongly with functional distance, while GCA correlated with monoculture biomass. The SCA can be calculated for different levels of diversity, if the proportion of originally planted individuals in the mixtures is known. GCA could be used in biodiversity-ecosystem functioning experiments when biomasses in monocultures for the species in the experiment are missing.

Our results are based on the interactions which occur on the aboveground fraction of the community and we may miss relevant competitive belowground interactions which determine part of the unexplained variability. However, asymmetric competition for light, which determines aboveground growth, explains the significant effect of functional distance on biomass, NE, SE and SCA.

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Tables

Table 1. SE, CE and NE in g/m^2 from all the pools and by species pool and treatment. Std.E is the standard error for the given effect. The overall values for the pools are presented in italics.

Pool	Treatment	SE	Std.E	CE	Std.E	NE	Std.E
All pools	Light	136.99	83.07	201.47	131.48	338.46	145.89
	Shade	84.56	20.95	18.48	26.89	103.04	41.00
	Overall	*110.97*	*43.02*	*110.65*	*67.77*	*221.62*	*76.65*
1	Light	-137.35	117.99	454.86	255.09	317.51	242.57
	Shade	99.12	37.07	42.71	66.53	141.83	91.78
	Overall	*-19.12*	*63.56*	*248.79*	*133.82*	*229.67*	*128.93*
2	Light	218.53	75.44	209.14	155.66	427.68	190.95
	Shade	-22.39	12.00	-46.66	22.71	-69.05	16.94
	Overall	*103.81*	*43.73*	*87.33*	*83.74*	*191.14*	*106.52*
3	Light	354.73	198.11	-82.63	247.59	272.11	320.18
	Shade	162.37	38.60	49.84	29.44	141.83	91.78
	Overall	*256.42*	*98.74*	*-14.92*	*120.93*	*241.49*	*157.60*

Table 2. Anovas for the dependent variables plot biomass, NE, SE and CE in 2-species mixtures (model type I). The combined biomass of the four central individuals in the plot was logged (and one outlier being more than four standard errors away from the mean was left out of the analysis). For the rest of the variables we took the square root of the absolute value and inserted the positive or negative sign of the original value to the transformed value. These transformations helped to meet the assumptions of constant within group variances and normally distributed residuals. The fixed terms which were fitted in the model were the light treatment (L-TR), the species pool (POOL), the functional distance between the species in the mixture (F-Dis), the presence of the dominant species within the mixture (DOM-MIX), the different mixtures without the presence of a dominant species (MIX). The individual terms were tested against the correct error terms (in italics) as indicated by Schmid *et al*. (2002). The table indicates the degrees of freedom (d.f.), F-ratio (F) and p-value (p). The "x" sign denotes interactions.

	Biomass		**NE**		**SE**		**CE**	
	F	p	F	p	F	p	F	p
L-TR	100.634	0.000	0.305	0.590	0.328	0.576	0.413	0.532
POOL	4.136	0.041	0.388	0.686	7.477	**0.007**	0.855	0.448
F-Dis	78.854	**0.000**	6.596	**0.023**	56.005	**0.000**	0.081	0.780
DOM-MIX	15.793	**0.002**	3.414	0.088	2.678	0.126	0.915	0.356
MIX	*1.809*	*0.149*	*0.740*	*0.703*	*1.496*	*0.239*	*1.011*	*0.492*
L-TR x POOL	4.374	**0.035**	3.309	0.069	14.994	**0.000**	1.943	0.183
L-TR x F-Dis	11.260	**0.001**	0.927	0.338	5.748	**0.018**	0.341	0.561
L-TR x DOM-MIX	3.797	0.054	0.030	0.863	0.449	0.504	0.155	0.694
L-TR x MIX	*1.465*	*0.144*	*1.045*	*0.416*	*0.749*	*0.710*	*1.163*	*0.318*
	d.f.=98[1]		*d.f.=99*		*d.f.=97*[2]		*d.f.=99*	

[1] One outlier (> four standard errors from the mean) excluded from data
[2] Two outliers (> four standard errors from the mean) excluded from data

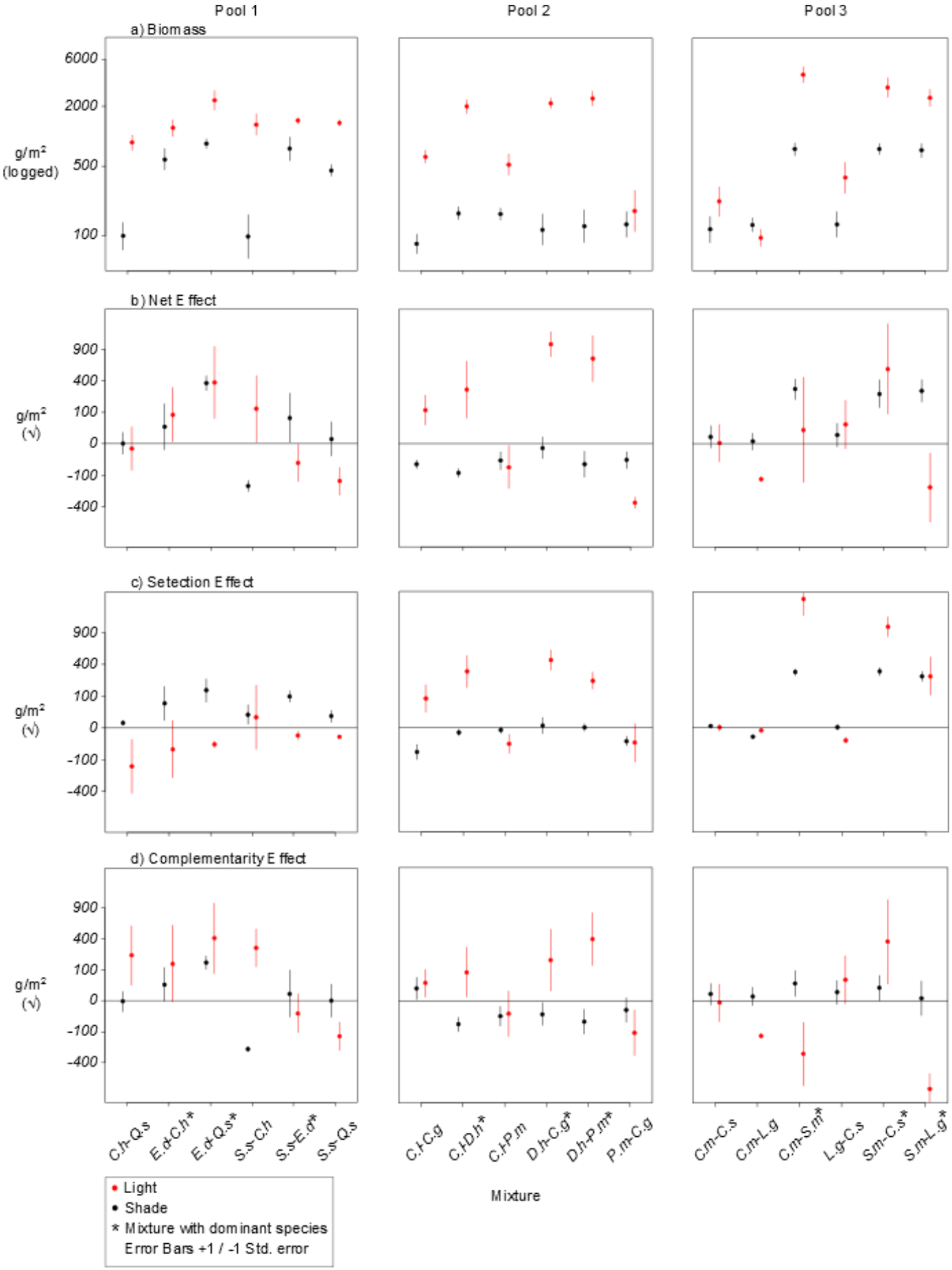
Table 3. Anovas for the dependent variables plot biomass, NE, SE and CE in two species mixtures (model type II). The combined biomass of the four central individuals in the plot was logged (and one outlier being more than four standard errors away from the mean was left out of the analysis). For the rest of the variables we took the square root of the absolute value, and inserted the positive or negative sign of the original value back to the transformed value. These transformations helped to meet the assumptions of constant within-group variances and normally distributed residuals. The fixed terms which were fitted in the model were light treatment (L-TR), the species pool (POOL), the dominant species within the species pool (DOM-SP), the non-dominant species (SP rest), the functional distance between the species in the mixture (F-Dis), the presence of the dominant species within the community mixture (DOM-MIX), the mixtures without the presence of a dominant species (MIX), the species as a fix term encompassing all the species level variables (SP aggregated) and the composition of the mixture as a fix term encompassing all the community level variables (MIX aggregated). The individual terms were tested against the correct error terms (in italics) as indicated by Schmid et al. (2002).The aggregated terms indicate the combined effect of the single terms if they would be added into one single term; individual terms reflect the specific effects of particular characteristics of the species and mixture composition. The table indicates the degrees of freedom (d.f.), F ratio (F) and p-value (p). The “x” sign denotes interactions.

	d.f.	Biomass		NE		SE		CE	
		F	p	F	p	F	p	F	p
L-TR	1	120.613	**0.000**	0.397	0.539	0.438	0.520	0.541	0.475
SP aggregated	11	14.064	**0.000**	1.085	0.381	6.429	**0.000**	1.066	0.396
POOL	2	6.781	**0.019**	1.232	0.342	9.568	**0.008**	2.239	0.169
DOM-SP	1	26.276	**0.001**	14.057	**0.006**	13.235	**0.007**	0.575	0.470
SP rest	*8*	*3.234*	***0.003***	*0.487*	*0.863*	*1.752*	*0.096*	*0.898*	*0.521*
MIX aggregated	15	15.672	**0.000**	2.019	**0.021**	5.326	**0.000**	1.679	0.067
F-Dis	1	36.997	**0.000**	6.936	**0.021**	31.849	**0.000**	0.064	0.805
DOM-MIX	1	9.305	**0.009**	4.048	0.065	2.265	0.156	0.675	0.426
MIX	*13*	*3.964*	***0.000***	*1.263*	*0.249*	*1.696*	*0.074*	*1.834*	***0.048***
L-TR x SP aggregated	11	4.035	**0.000**	1.884	0.050	4.894	**0.000**	1.507	0.141
L-TR x POOL	2	5.877	**0.027**	8.350	**0.011**	23.856	**0.000**	4.818	**0.042**
L-TR x DOM_SP	1	0.597	0.462	0.323	0.585	1.429	0.266	0.030	0.868
L-TR x SP rest	*8*	*2.181*	*0.035*	*0.828*	*0.580*	*0.942*	*0.486*	*0.939*	*0.489*
L-TR x MIX aggregated	15	3.298	**0.000**	1.480	0.127	1.533	0.108	1.580	0.093
L-TR x F-Dis	1	5.708	**0.033**	0.774	0.395	7.005	**0.020**	0.229	0.640
L-TR x DOM-MIX	1	1.519	0.240	0.042	0.841	0.443	0.518	0.127	0.728
L-TR x MIX	*13*	*2.445*	***0.006***	*1.606*	*0.096*	*1.125*	*0.348*	*1.775*	*0.058*
		d.f.=98[1]		*d.f.=99*		*d.f.=97*[2]		*d.f.=99*	

[1] One outlier (> four standard errors from the mean) excluded from data
[2] Two outliers (> four standard errors from the mean) excluded from data

Figures

Fig. 1. Performance of 18 2-species mixtures of three species pools of four species each, growing in two different light conditions with regard to a) biomass, b) NE, c) SE and d) CE. Graphs show raw data. Each mixture was replicated 4 times. Species in species pool 1: 1: *Castanea henryi* (*Ch*), *Elaeocarpus decipiens* (*Ed*), *Quercus serrate* (*Qs*) and *Schima superba* (*Ss*); species pool 2: *Cunninghamia lanceolata* (*Cl*), *Pinus massoniana* (*Pm*), *Sapindus mukorossi* (*Sm*) and *Cyclobalanopsis glauca* (*Cg*); and, species pool 3: *Lithocarpus glaber* (*Lg*), *Cyclobalanopsis myrsinaefolia* (*Cm*), *Castansopsis sclerophylla* (*Cs*) and *Dalbergia hupeana* (*Dh*).


Pool 1
Pool 2
Pool 3
a) Biomass
g/m²
(logged)
6000
2000
500
100
b) Net Effect
g/m²
(√)
900
400
100
0
-100
-400
c) Setection Effect
d) Complementarity Effect
C.h-Q.s
E.d-C.h*
E.d-Q.s*
S.s-C.h
S.s-E.d*
S.s-Q.s
C.l-C.g
C.l-D.h*
C.l-P.m
D.h-C.g*
D.h-P.m*
P.m-C.g
C.m-C.s
C.m-L.g
C.m-S.m*
L.g-C.s
S.m-C.s*
S.m-L.g*
Mixture
Light
Shade
* Mixture with dominant species
Error Bars +1 / -1 Std. error

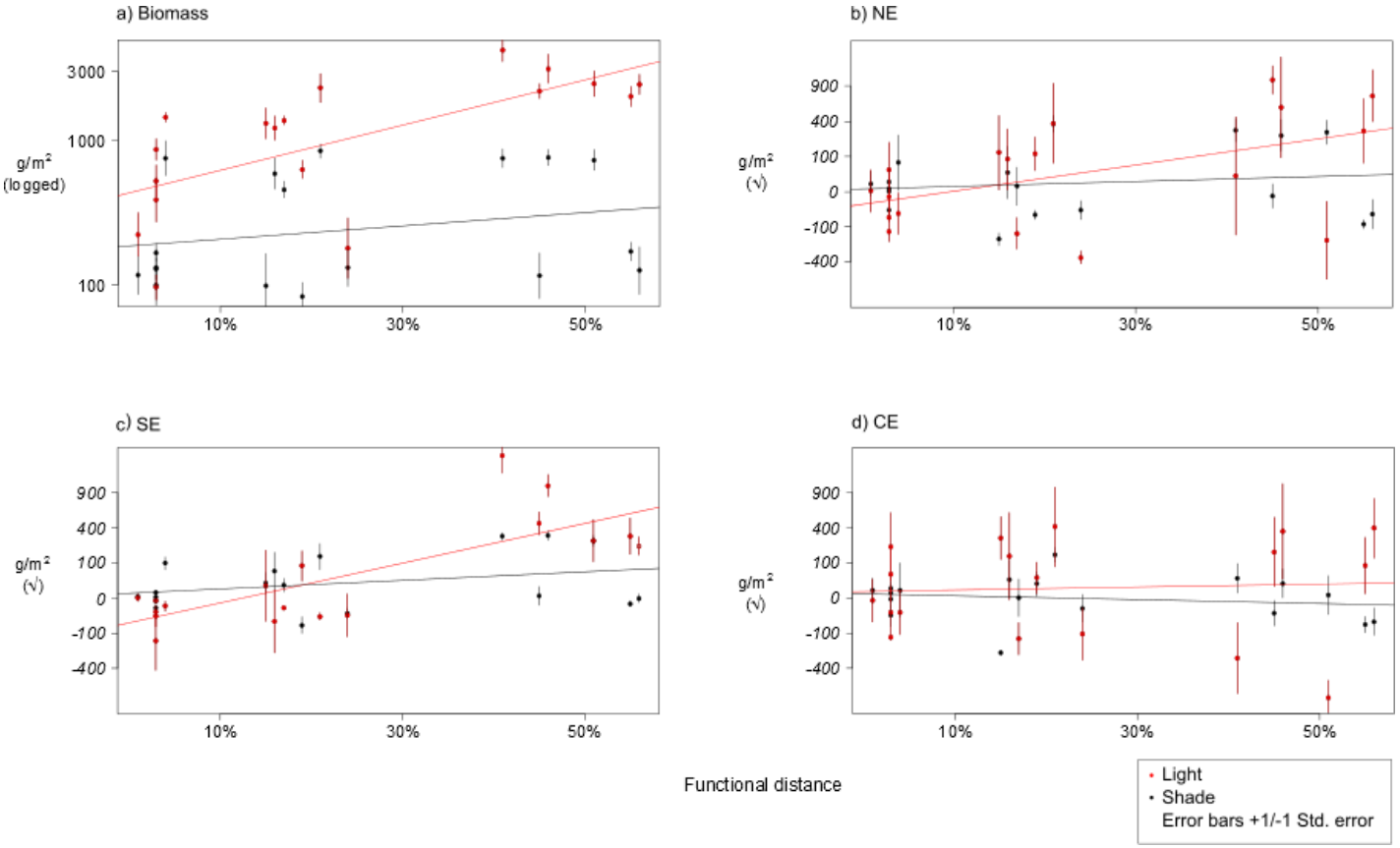


Fig. 2. Relationship of functional distance between 18 2-species mixtures growing in two different light conditions with regard to a) community biomass, b) NE, c) SE and d) CE. Graphs show raw data. Each mixture was replicated 4 times.

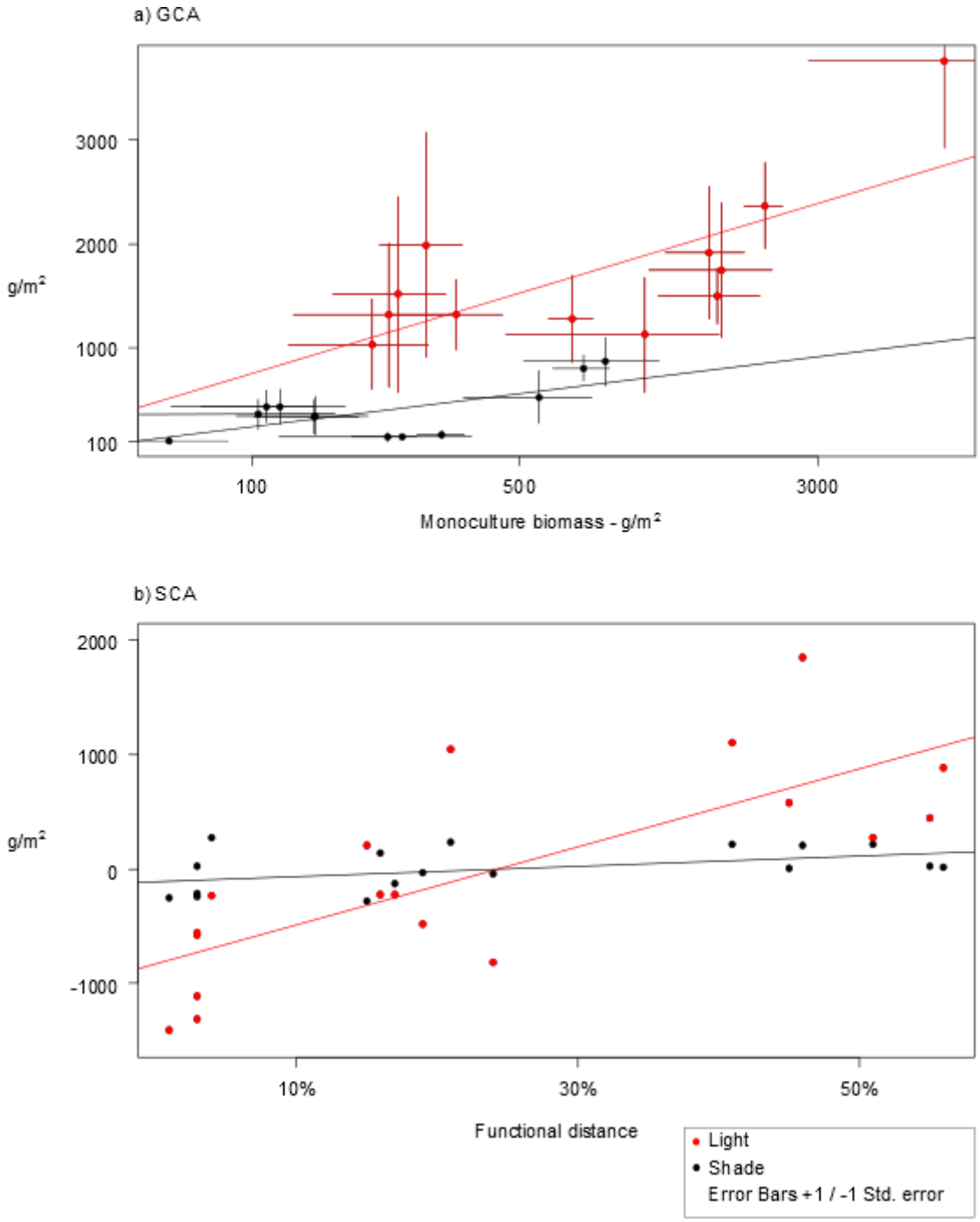
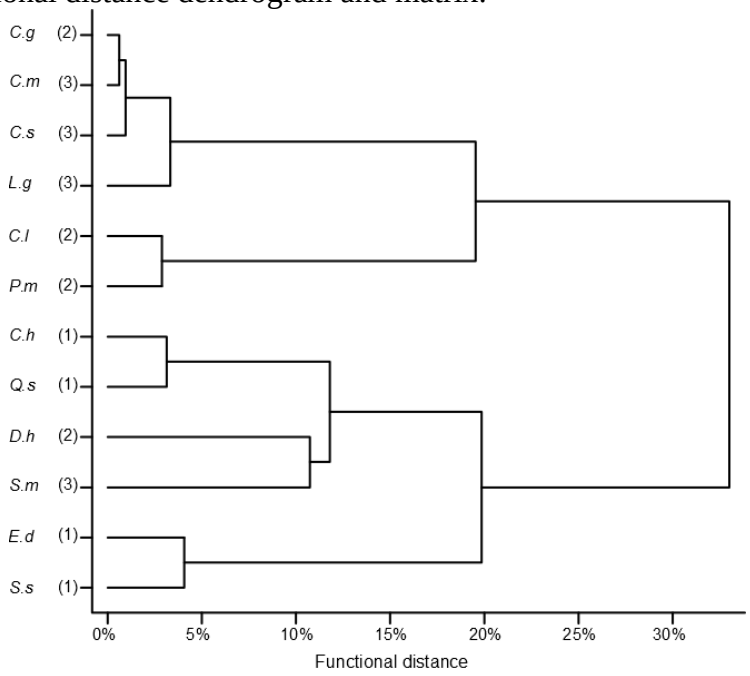


Fig. 3 Comparison of 18 2-species mixtures growing in two different light conditions according to a) biomass of the individual species growing in monoculture and their general combining ability (GCA), which is the average biomass of the species across all the mixture combinations; b) functional distance between the two species in the mixture and their specific combining ability (SCA), which is the deviation of the biomass of each mixture from the expected biomass determined by the GCA. Each mixture and monoculture was replicated four times.

Appendix

Appendix 1. Functional distance dendrogram and matrix.



Similarity dendrogram. Nodes closer to one, show higher degree of functional similarity than nodes closer to zero. The two letters in front of each line represent the species. Pools to which the species belong are indicated in parentheses. Species in species pool 1: *Castanea henryi* (*C.h*), *Elaeocarpus decipiens* (*E.d*), *Quercus serrate* (*Q.s*) and *Schima superba* (*S.s*); species pool 2: *Cunninghamia lanceolata* (*C.l*), *Pinus massoniana* (*P.m*), *Sapindus mukorossi* (*S.m*) and *Cyclobalanopsis glauca* (*C.g*); and, species pool 3: *Lithocarpus glaber* (*L.g*), *Cyclobalanopsis myrsinaefolia* (*C.m*), *Castansopsis sclerophylla* (*C.s*) and *Dalbergia hupeana* (*D.h*).

Pool	Species	1				2				3			
		C.h	*E.d*	*Q.s*	*S.s*	*C.l*	*C.g*	*D.h*	*P.m*	*C.m*	*C.s*	*L.g*	*S.m*
1	*C.h*												
	E.d	**16.3**											
	Q.s	**3.1**	**20.7**										
	S.s	**15**	**4.1**	**17.3**									
2	*C.l*	37.9	33.2	37.0	22.6								
	C.g	25.1	25.3	19.1	13.2	**18.7**							
	D.h	44.7	19.1	14.6	18.3	**55.4**	**44.7**						
	P.m	38.5	28.3	36.9	22.8	**2.9**	**24.3**	**55.7**					
3	*C.m*	24.1	23.7	18.2	12.5	19.2	0.6	42.9	24.2				
	C.s	23.7	23.0	19.2	12.9	16.9	0.8	45.4	21.5	**1.2**			
	L.g	30.1	28.2	23.5	17.5	17.6	4.2	53.6	19.7	**2.9**	**3.1**		
	S.m	13.5	25.6	11.0	26.5	64.9	42.7	10.7	61.5	**40.5**	**45.9**	**51.0**	

GENERAL DISCUSSION

In this study I focused on species diversity–productivity relationships in subtropical forests. Specifically I assessed the aboveground component of tree communities to determine whether the positive effect of tree species diversity on community biomass is consistent and occurs irrespective of the successional stage of the community. In a comparative study of secondary forests I found a consistent positive diversity–productivity relationship in two size cohorts at all successional stages (Chapter 1). I experimentally assessed the effects of species richness and density on sapling growth patterns. Species richness enhanced self-pruning and branch turnover, but had little effect on canopy biomass, crown area or number of branches of saplings (Chapter 2). Furthermore, I found that species richness had a positive effect on community biomass in direct sunlight and in the shade mediated by the presence of dominant species (Chapter 3). In addition, I found that particular compositions of the mixtures had positive effects on crown length and area (Chapter 2) and on community biomass (Chapter 3). Finally, in an in-depth analysis of the ecosystem functioning effects of species composition in 2-species mixtures, I determined that a greater functional distance between the species in the mixture had a positive effect on community aboveground biomass, the net effect and the selection effect (Chapter 4).

Diversity–productivity relationship

Despite results from observational studies suggesting a similar positive diversity–productivity relationship in forests as has been experimentally demonstrated in grasslands (Hooper *et al*. 2005, Balvanera *et al*. 2006, Cardinale *et al*. 2006), many BEF (biodiversity–ecosystem functioning) studies focusing on mature forests lack proper experimental design. Such studies, carried out in managed or planted forests, have determined diversity–productivity correlations rather than cause–effect relationships (Nadrowski *et al*. 2011). We faced similar challenges: BEF forest experiments are relatively young in contrast to mature natural forests. Surveys tend to

accumulate sample units towards mean diversity levels, and are besides affected by non-controlled confounding factors.

In this thesis I used a comparative study (Chapter 1) to avoid the design limitations encountered with surveys of mature forests. In such a comparative study variables are treated as independent by searching and fixing units for particular levels a priori. We actively searched for pre-selected levels of species richness (i.e low, medium and high diversity) in each of pre-established successional stages. The distribution of the data points along the range of values are balanced by fixing the variables to pre-established levels, which permits species richness and successional stages to be treated as independent variables (Snedecor & Cochran 1989). In addition, I controlled for strong edaphic differences and other environmental factors by including two principal components from a PCA (principal components analysis) of a number of abiotic factors, such as elevation, slope aspect, slope inclination, soil pH, soil moisture, and soil organic C and N.

In the comparative study, I demonstrate a positive diversity effect on productivity (basal area increment) and biomass (basal area) of different successional stages of forest stands. As measure of diversity I used species richness; however functional and phylogenetic diversity were strongly correlated with species richness and gave similar results. In contrast, evenness was negatively correlated with species richness and therefore negatively related to basal area and basal area increment. These results were consistent for two cohorts of stems; trees between 3 and 10 cm DBH (diameter at breast height) and trees above 10 cm DBH. In each cohort diversity was calculated for the individual species/trees occurring within the cohort.

Under experimental conditions, in Chapter 3, I demonstrate a positive diversity–productivity relationship in both the light and the shade treatment. Species richness had a significantly positive effect on biomass of sapling communities illustrated by the greater biomass harvest of 2-

and 4-species mixtures in contrast to the biomass harvested from monocultures. In each of the three species pools, one species showed dominance, producing a larger biomass, height and basal diameter at harvest than the other species in the species pool in both monocultures and mixtures. The diversity–productivity relationship in this experiment was therefore mediated by the presence of a dominant species within each species pool. When I analyzed the 2-species mixtures, I found that the dominant species, the presence of the dominant species in the mixture and the functional distance between the species in the mixture had a positive effect on biomass production, net effects and selection effects.

In the experiment focusing on species richness–density relationships, we found a direct effect of species richness on branch demography; specifically pruning and branch turnover increased as species richness increased (Chapter 2). Such an effect suggests a process of niche differentiation within the community, via competition for and adaptation to light conditions. As with the results of the light treatment experiment (Chapter 3), species composition emerged as a relevant attribute of the community. *Castanea henryi* and *Q. serrata* accumulated greater total biomass when in a mixture in combination with *E. decipiens*, in contrast to the biomass produced in monocultures and in mixtures with other species.

Diversity–productivity and light conditions

Individual plants compete for resources (Weiner 1990), or facilitate resource access for other individuals (Brooker *et al*. 2008). The nature of intra- and inter- specific plant interactions is determined by the availability of resources (Brooker *et al*. 2008). Light is the major resource for which plants compete aboveground (Newman 1973). Differences in light availability therefore strongly affect productivity in plant communities. Such differences in light availability are reflected in nature, for example in secondary successions or forest understory plant communities. Although the understory may experience light limitations, the canopy cover and species

composition may increase availability of other resources, such as humidity or soil organic matter (Lemenih *et al*. 2004.).

In chapter 1, I demonstrate there is a positive effect of species richness on basal area increment for both cohorts. The two cohorts presented a negative diversity correlation. As the smaller cohort, 3 −10 cm DBH, is present predominately in the understory (except for young forests, in which trees in this cohort would also be part of the canopy layer) it is conceivable that this negative correlation was determined by the light availability.

In chapter 3, I assess the growth of saplings in two light treatments, light or shade. The light treatment simulated interactions of species within communities growing in a secondary succession (direct sunlight) or in the understory (shaded communities). I found a positive effect of species richness on community biomass in both treatments. In the shade treatment, community biomass was consistently lower in contrast to the biomass of communities grown in the light treatment due to species-specific survival and growth conditions in the two different light conditions.

Density, a result of diversity or a confounding factor?

In Chapter 1 I show a density-mediated diversity effect on growth and therefore hypothesize that diversity could promote density as a result of complementarity between species as has been experimentally demonstrated in herbaceous communities (Marquard et al. 2009). Density alone may increase competition thereby reducing individual growth; however, by increasing the number of individuals in a given area, density can increase community biomass. Although density was not evaluated in the light treatment experiment, the trend was towards a slight reduction of mortality in species-rich mixtures, suggesting a decrease in competition in species-rich mixtures. I manipulated species richness and density in a factorial experiment and

found density reduced individual growth. Neither species richness nor the interaction between species richness and density influenced individual biomass.

I did not prove a causality in the species richness−community density relationship. For example, an increase in the number of individuals within a community increases the chances of finding more species. I assessed this possibility indirectly in the structural equation model by alternating the direction of the causality. The results show stronger significance when species richness was considered independent of density, suggesting a species richness effect on density rather than vice versa.

Diversity mechanisms: the role of functional traits

In chapter 4, I explore the interactions in 2-species mixtures. Although selection effects (SEs), complementarity effects (CEs) and net biodiversity effects (NEs) were on average positive, only SEs were significantly greater than zero. Functional distances between species in 2-species mixtures had a positive effect on total biomass, net effect (NE) and selection effect (SE). Extreme trait variation can define interspecific differences in productivity and the dominance of the most productive species in the community (Loreau 2000). Dominant species, consistently located functionally distant from the other species in the species pool, holding extreme trait values, in height, diameter and biomass production. Functional distance also has a significant effect on NE and biomass production, which probably was mainly due the positive SE.

Niche differentiation in my study did not appear to increase complementarity between species but rather seemed to reduce competition for dominant individuals supported by the significant influence of functional distance on SE and similarly on NE and total biomass. Our experiment lasted for eighteen months, which represents only a short period in the life cycle of plant communities; it may be that CEs would become more important later in community development.

This has been found to be the case in meta-analysis of other BEF experiments (Cardinale *et al*. 2007).

BEF perspectives

Most of the conclusions of BEF theory have been developed for grasslands and microcosms, which is a consequence mainly of logistical considerations (Balvanera *et al*. 2006). BEF experiments require a wide diversity gradient with sufficient intermediate diversity levels and replicates. In addition, confounding factors (i.e. edaphic conditions, soil nutrients) in BEF forest experiments imply the need of a random spatial distribution of the diversity levels which, due to space constraints, are difficult to control in forest stands (Nadrowski *et al.* 2011). These challenges determined an earlier establishment of long-term BEF grassland experiments, which have been running for over twenty years, whereas the first forest BEF experiments were planted less than fifteen years ago (http://www.treedivnet.ugent.be/experimental.html).

BEF experiments are used to assess different forest functions independently. Although meta-analysis (Hooper *et al*. 2005, Balvanera *et al*. 2006, Cardinale *et al*. 2011) have tried to link multiple effects together, it is not yet known if and how diversity effects may be inter-linked. It would be interesting to evaluate how the positive effects of diversity on a particular ecosystem function may affect others functions at different organizational and trophic levels.

Although functional trait roles are explained partially in grasslands (Flynn *et al*. 2011), there are fewer experimental results in forests systems. Determining what combination of traits determine particular species compositions which produce stronger effects in biomass production, and how they influence CE and SE in forests, is necessary to understand the precise role of traits in multiple species interactions.

Considering the longevity of trees and forests stands, it will be decades until definitive results from experiments on mature forests will be available. Intermediate results are providing insights into species interactions and trends in diversity−ecosystem relationships functioning at intermediate forest development stages. There is a great need for the results of BEF experiments in forests to better understand tree species coexistence in forests and therefore more accurately predict the effects of loss of biodiversity in forests. We should nevertheless continue to assess species diversity effects in natural conditions which will further deepen our understanding of species coexistence and the consequences of species loss on ecosystem functioning in forests under natural conditions.

Finally, BEF analysis may yet be optimized by considering alternative analytical approaches. The mechanistic diallel analysis has been proposed but not yet been used in BEF analysis (Schmid *et al*. 2002). Such an analysis would allow the detailed study of the effect of the presence of particular species using a basic design (logistically simple) alternating the target–neighbor's identity and manually correcting the degrees of freedom. By using general and specific combining ability, it would be possible to partially neutralize the effect of species which largely overperform in monocultures. Although advances in statistical analysis have allowed comprehensive BEF theories, there is room for optimizing calculations to clarify in-depth results through alternative statistical approaches.

BEF practical applications / considerations for forest management and restoration

Twenty years of research has provided evidence for the role of biodiversity in ecosystem functioning. Biodiversity has been found to enhance productivity in grassland ecosystems and recently in forest ecosystems.

In the context of global biochemical cycles (Bala *et al*. 2003), being among the most productive world ecosystems (Dixon *et al*. 1994) and covering roughly a third of land area (FAO 2010),

forest ecosystems are of vital importance. Moreover, considering the world mass extinction we experience (Chapin *et al*. 2000), forest diversity levels and forest area transformation (Malhi *et al*. 2008) determine the relevance of BEF in forest and particularly in highly diverse ones.

In the light of diminishing natural forest covers, intensifying towards the tropics (Vitousek *et al*. 1997, Wright & Muller-Landau 2006, Aerts & Honnay 2011), such research is increasingly relevant. The situation in China is not as severe as in other countries due to the afforestation projects, which balance the forest cover reduction for the whole continent (FAO 2010).

There are therefore two important considerations. Firstly, natural or semi-natural old diverse forests should be assessed and protected. Old forests possess complex structures, which only develop over successional stages. If such structures (i.e. diversity, plant composition, height, vertical strata, light interception, soil composition, depth, etc.) promote conditions which enhance one or several ecosystem functions, they offer an excellent opportunity for forest community research but would also constitute a particularly interesting system for conservation purposes. Secondly, it is also highly important to be aware for which purpose a forest is planted; naturally occurring forests should not be confused with forest planted for wood production. Although the express purpose of a planted forest may not be for the ecosystem services it provides, it may yet have a relative value as a provider of ecosystem services. Whether the purpose of a planted forest is providing ecosystem services, other uses or mixed uses, the management plan of such a forest has an outcome on the ecosystem services it may provide (Paquette & Meissen 2010). Forest plantations have traditionally been composed of one or few tree species, because the management and harvesting logistics of one species is more profitable (Piotto *et al*. 2010). However, a species-rich forest plantation or a plantation in which the growth of other tree species is allowed and encouraged could offer additional ecosystem services (Yachi & Loreau 1999, Isbell *et al*. 2011, Aerts & Honnay 2011).

I have seen how diversity increases productivity on one hand. However, diversity has effects on additional ecosystem functions. BEF in forests are producing first results and although it is too early to draw definitive conclusions on other ecosystem functions, management decisions in forests should be founded on the preliminary results.

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